Ontogenetic Niche Shifts Within Floodplain Meadow Species

Thesis

Ontogenetic niche shifts within floodplain meadow species

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Abstract

Ontogenetic niche shifts, (ONSs), or changes in niche breadth or position during development, can be a critical component of effective target-species conservation, as long-term survival demands that the intergenerational requirements of species be fully met. However, although ONSs could occur in 80% of animal taxa, previous studies have rarely involved plants, and those that do exist have often been hampered by the lack of long-term, field-based data or appropriate measures. Analysis of the twenty years of botanical and hydrological data collated by the Floodplain Meadow Partnership, in combination with a multi-site, fully factorial planting experiment with two levels of competition, allows the following questions to be addressed; a) are ONSs occurring within floodplain meadow species, including the scarce *Fritillaria meleagris*, and how can the hydrological regime driving such shifts be quantified? b) Does flooding enhance recruitment within a range of meadow species? and, c) what are the mechanisms underlying flood-related gap creation? Results revealed that occurrence of ONSs varies according to species. Abundance of juvenile fritillaries was correlated with interquartile range in water-table depth prior to parental seed dispersal, suggesting micro-site limitation, with subsequent generations associated with predominantly

dry conditions. Further differences in associate species and community membership of juveniles versus flowering adults were detected, which, results suggested, may be due to differential soil profile characteristics or other legacy effects. Seasonal as opposed to annually-derived hydrological variables were of particular relevance to the study of ONSs, and spring of the year before survey identified as the critical period for germination of all the selected species. Whereas flooding enhances recruitment and appears to drive ONSs within both *Fritillaria meleagris* and *Leontodon autumnalis,* germination of the obligate hemi-parasite *Rhinanathus minor* decreased in gaps lacking host species. A correlation between die-back of flood-sensitive grasses following flood-events and increased fritillary juvenile abundance was established.

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Chapter 1

Introduction

This chapter introduces the theme of ontogenetic niche shifts within floodplain meadow species, their relevance to conservation, and the overall layout of the thesis.

1 Introduction

1.1 Ontogenetic niche shifts

Ontogenetic niche shifts, (ONSs), or the changes that occur in niche breadth or position during development, are thought to profoundly influence population dynamics and community structure within ecosystems (Cavender-Bares and Bazzaz 2000; Miriti 2006), and knowledge of which taxa undergo such shifts is therefore of central relevance to initiatives aiming to effectively conserve or manage the long-term survival of target species and communities. However, whereas ONSs represent a well- documented phenomenon within the animal kingdom, with as many as 80% of taxa thought to exhibit such shifts, (Ebenman, Persson et al. 1988), studies within plants remain comparatively rare, (Eriksson 2002; Young, Petersen et al. 2005). Previous accounts of plant niches have tended to focus on only the adult stage of species, or combined all age-states together, and those that have dealt with ONSs have been largely lab- or mesocosm-based, involving single species or using data of only short duration, (Parrish and Bazzaz 1985; Quero, Gomez-Aparicio et al. 2008). This study aims to establish whether

ontogenetic niche shifts occur within a range of UK floodplain meadow species, including the Nationally Scarce *Fritillaria meleagris*, (Snake's Head Fritillary), and by a combination of field experimentation and analysis of an extensive, long-term database, investigate the role of flooding and associated mechanisms in relation to successful recruitment.

Ontogenetic niche shifts are thought to occur when resource-requirements or tolerances to external factors change according to developmental age, resulting in differential rates of mortality, growth or reproductive allocation, and rendering each age-state a functionally distinct group, (Eriksson 2002; Quero, Gomez-Aparicio et al. 2008). In such cases where they occur, shifts can be characterised either by; a) a niche expansion, where biotic/abiotic requirements are stricter during early developmental stages, b) a niche contraction, where requirements become narrower through ontogeny, or c) an abrupt change in niche-position altogether, with subsequent stages responding to a completely different biotic or abiotic driver. In the search for general rules about ONSs, many studies have concluded that particular plant groups are dominated by one or other of these expressions, whereas a few have found the presence and form of niche shift to be entirely dependent on the species in question, (Eriksson 2002). Within the plant kingdom, ONSs

have been documented within old-field annuals, (Parrish and Bazzaz 1985), shrubs, (Eriksson 2002; Miriti 2006), and trees, (Quero, Gomez-Aparicio et al. 2008; Bertrand, Gégout et al. 2011), with shifts occurring along several environmental gradients, including moisture, temperature, light, nutrients and neighbour proximity. However, to my knowledge, there have been as yet no field-based studies describing the occurrence and form of ONSs within UK floodplain meadow species, and the relative importance of flood-related disturbance as a driver for ontogenetic niche shifts remains comparatively untested.

1.2 The niche versus neutral debate

The term, "ontogenetic niche shifts", was coined only relatively recently, (Parrish and Bazzaz 1985), and is set within the context of a much wider, controversial and long-standing theoretical debate regarding the relative contribution of niche versus neutral or stochastic processes to modes of community assembly and mechanisms of co-existence. The deterministic, niche-based approach assumes that species partition resources and segregate along predictable trajectories, determined largely by environmental conditions and competition, (Clements 1916; Diamond and Case 1986; Keddy 1992; Diaz, Cabido et al. 1998), whereas the stochastic

approach states that composition is determined only by chance colonisation, extinction and ecological drift, (Egler 1954; Drake 1991; Lanta and Lepš 2009). Questions remain regarding the relative contribution of each to floodplain meadow assembly.

Critics have argued that classical niche theory fails to take into account either dominance-tolerance trade-offs or the unpredictable forces governing community assembly, including fluctuating disturbance, dispersal effects, feedbacks, abundance in the species pool and historical legacy, (Drake 1991; Hubbell 2001; Temperton 2004; McGill, Enquist et al. 2006). Two niche concepts that do include temporal fluctuation, however, are the "storage effect", (Chesson and Warner 1981), and the "regeneration niche", (Grubb 1977; Nakashizuka 2001); both closely linked to the concept of ONSs.

The storage effect describes the ways in which individuals benefit from changes in environmental conditions from year to year, storing the gains from favourable years, and buffering against the effects of bad years, thereby ensuring persistence and co-existence, (Chesson and Warner 1981), and represents a concept that has gained considerable popularity

in recent years, (Terradas, Peñuelas et al. 2009). The storage effect is thought to collapse when a threshold within the required bounds of variation of the driver is exceeded at some stage during the life-history of species, resulting in competitive exclusion and local extinction. The "regeneration niche" recognises the significance of different strategies and dispersal traits including seed vector, weight and number for recruitment for the first time within niche-theory, but it focuses on only the early stages of the species' life-cycle, whereas ONSs recognises the importance of all age-states to assembly and long-term survival.

A growing body of research that unites both "niche" and "stochastic" schools of thought is the view that abundance in the species pool, and dispersal traits in combination with niche-segregation may offer the most valid explanation of community assembly. As the majority of floodplain meadow species are relatively frequent in the wider landscape, seed limitation seems unlikely to represent a major factor limiting recruitment in traditionally managed floodplain meadows, but there has been little field-testing of the recent theories to date. This has been due largely to the difficulties in actually defining niches and quantifying the key drivers of change - especially those relating to disturbance dynamics, and it is broadly accepted that, "knowledge of the relative importance of niche-

based and dispersal processes under varying conditions remains fragmentary", (Ozinga, Schaminée et al. 2005).

1.3 Recruitment-limitations and the role of flood

Disturbance has been defined as, "relatively discrete events in time that disrupt the ecosystem, community or population structure and bring about change in resources, substrate availability or physical environment", (White and Pickett 1985), and the impacts of such events can be cumulative, hierarchical, or interact with other drivers across different temporal scales, (Mori 2011). On meadows, flooding can transport sediment, nutrients and litter, cause mechanical damage and anoxia, interrupt important life-cycle events and lead to the elimination of flood-intolerant species, but can also serve as a vector for propagules, determine both the number and type of "safe sites" available for subsequent colonisation, (Harper, Williams et al. 1965), and favour those species with trait-adaptations or strategies to tolerate waterlogging, (Grime, Hodgson et al. 1989). Flooding is thus thought by many to represent a key filter within floodplain meadow communities, influencing species diversity, relative competitive ability and community composition, (Tockner, Malard et al. 2000; Toogood and Joyce 2009; Kotowski,

Beauchard et al. 2010), although there remains little direct experimental evidence examining the varying impacts of flood in relation to recruitment and later stages of ontogeny within meadow species, and opinions diverge regarding both the critical timing of such events and consequently the most appropriate time-scales of hydrological variables with which to study them.

Whereas some studies have found that germination occurs only in vegetation gaps in floodplain meadows, (Kotowski, Beauchard et al. 2010), and that productive habitats such as these are correspondingly microsite- or niche-limited, (Hughes, Adams et al. 2001; Lanta and Lepš 2009), others conclude that germination can also take place in dense vegetation, (Jensen and Schrautzer 1999), and have identified dispersal as the primary limitation, (McDonald 1993; Moore and Elmendorf 2006). However, a report detailing results of the 2010 annual botanical survey, following flooding, and collated on North Meadow NNR by the Floodplain Meadow Partnership, (Wallace 2010), suggests that meadow community assembly may be related to both niche and stochastic processes.

The report indicated that in areas subject to moderate levels of flooding, species with high Ellenberg indicator values for moisture and tolerance of waterlogging had persisted and increased, but that the blocks that had been the most severely affected had also subsequently displayed an increase in "dry" species with low moisture values. Many of the latter were annuals or ruderals, and it was suggested that the gaps created in the most severely affected areas by die-back of flood-sensitive species, namely some types of grasses, could be enabling these more opportunistic species to rapidly colonise.

The findings appear to indicate that the communities involved were displaying a shift from predominantly hydrologically-defined niches to those determined by both micro-site availability and dispersal-traits beyond a certain threshold of stochastic flood-severity. Knowing which species are likely to be affected by such processes, and when, is considered to be of particular importance to conservation projects as it enables time and resources to be managed effectively, (Trowbridge 2007).

Species possessing certain strategies and traits relating to seed and seed-bank characteristics have long been known to be favoured by flood

events, (McDonald 1993; Holzel and Otte 2001; Hölzel and Otte 2004). Persistent seed banks are understood to represent an adaptation to high interannual variation in ecological conditions, (Leck and Simpson 1987; Klimkowska, Van Diggelen et al. 2009), and indeed, species usually subordinate in the community containing fritillary, that are well represented in the seed bank, such as *Poa trivialis* and *Agrostis,* are known to increase exponentially in cover following extreme flood events, (Hölzel and Otte 2004).

Ruderals and species with numerous, wind-dispersed seeds, including members of the *Compositae*, often also benefit following flooding, (Grime, Hodgson et al. 1989), though viability can be poor if waterlogging persists. The heavier, transient seeds associated with many competitive perennials are thought to place them at greater risk of local extinction, if extreme conditions persist, (Smart, Bunce et al. 2005), but that during more moderate, shorter-term flood-events, large seeds adapted to hydrochory, have a competitive advantage as they possess a greater tolerance of shading during the germination stage, in addition to a longer viability in water.

Extensive and prolonged flooding over consecutive years, particularly when hay-cuts are missed, can severely alter the nutrient balance on meadows and favour species with additional strategies adapted to waterlogging, such as the aerenchyma-formation or rhizomes associated with several invasive *Carex* species. Many of our richest meadow sites have witnessed a radical shift to *Agrostis-Carex* swamp communities in recent years, limiting the capacity of less competitive herbs to recruit, and resulting in a homogenous, species-poor, vegetation-type. The relative importance of niche versus dispersal limitation on meadows thus appears to be related both to species and to flood-severity; the latter defined by both the scale and timing of such events, but further investigation is required to quantify these drivers.

1.4 The relevance of timing

One of the few deterministic methods that have been devised and successfully applied to quantify niches to date is that of Sum Exceedence Values, or SEVs, (Gowing and Spoor 1998); a technique that describes the degree to which the water table exceeds the thresholds for aeration and drought stress experienced by species, enabling species and community realised niches to be quantified along an ecohydrological axis. The

aeration stress threshold is determined by the exact depth of the water table at which roots becomes waterlogged, and the threshold for drought stress calculated as the depth at which plants begin to exhibit water stress, (Gowing and Spoor 1998 ; Araya, Silvertown et al. 2011), with the resulting values for extent and duration of these exceedences summed by year produce an SEV.

One of the key advantages of such a method is that it allows for incorporation of local climate data and soil hydraulic properties and is therefore transferable between sites, and it has been applied to quantify the niches of many communities on floodplain meadows, but it remains unknown whether annually-averaged SEVs represent an appropriate measure to correlate with the niche responses of age-states, which seem likely to be operating on much finer time-scales than this. Critics also argue that SEVs do not sufficiently account for seasonal variability in rainfall and temperature, and that the specific timing of floods is of key significance to species survival, - (Aarssen and Epp 1990; Grevilliot, Broyer et al. 1998; Whited, Lorang et al. 2007; Bartholomeus 2010; Penuelas, Terradas et al. 2011), - reflecting a wider concern that the temporal aspects of hydrological regime have not yet been, "satisfactorily integrated into practical application", (Mori 2011).

The seasonal timing of flood events is thought to be of particular relevance to age-state survival as relative tolerances and competitive ability are considered to be largely age-dependent, - (Aarssen and Epp 1990; Grevilliot, Broyer et al. 1998; Hughes, Adams et al. 2001; Kennedy, Milne et al. 2003; Suding and Hobbs 2008), - but there exists some degree of debate regarding the relative impact of spring versus summer flooding in relation to recruitment and persistence. Whereas some researchers have identified the hydrological regime during germination and seedling establishment stages as particular bottlenecks for survival and establishment, (Grubb 1977; Grime 1979; Kotowski, Beauchard et al. 2010), others have found conditions associated with the reproduction stage to be of key importance to species persistence, (Hughes, Adams et al. 2001).

As soil moisture influences both temperature and degree of microbial activity within the soil, the timing of flood events influences the onset of spring growth and degree of neighbour-competition experienced by seedlings. Seedlings are thought to be more sensitive to competition and harsh abiotic conditions than adults, (Grime 1979), and so floods late in spring, with associated mechanical damage and burial by sediment, or even subsequent water draw-down that is too rapid, can lead to high rates

of mortality within this group early in the year, (Bendix and Hupp 2000; Hughes, Adams et al. 2001). However, flooding in summer can also exponentially increase rates of mortality due to anoxia, and lead to large-scale losses of viable flowers, affecting both the quantity and content of seed input from seed rain and hydrochory. Persistence depends on the ability of species to complete all key stages of their life-cycle within the required time-scale, and thus establishing how each age-state is likely to impacted by floods of various timings and magnitude, and how this differs between species, is therefore of key importance to conservation initiatives.

As the tolerances of age-states, species and communities can vary in relation to the timing of flood events, the timing of responses to flood events would also seem likely to vary according to species and age-state; with long-lived species displaying longer lags than those possessing a short life-cycle, for example. However most previous studies of the relationship between species and environment have omitted ontogenetic concerns or been hampered by the use of only short-term time-series analysis or inappropriate data measures, (Gowing 2002; MacDougall, Wilson et al. 2008; Toogood and Joyce 2009). Establishing the different time-lags displayed by different floristic measures of a variety of species in response

to key drivers could prove very informative when determining the major factors limiting recruitment and species persistence, and floodplain meadows provide an ideal habitat in which to examine these questions further.

1.5 Floodplain meadow conservation-status

Floodplain meadows represent a valuable component of the UK's lowland cultural landscape. Traditionally managed sites can contain as many as 38 plant species per square metre and provide key habitats for six Nationally Rare species of *Taraxacum*, nationally important assemblages of breeding and wading birds as well as an array of uncommon invertebrates, (Woodcock, McDonald et al. 2011). In addition to biodiversity, floodplain meadows serve important social, economic and ecosystem functions including production of a valuable hay crop, flood alleviation and water quality improvement in the broader environment, (Mountford, Roy et al. 2006), and thus there are many incentives to conserve and maintain them.

The most species-rich of the floodplain meadow plant communities, defined as the type MG4, or *Alopecurus pratensis – Sanguisorba officinalis* grassland within the National Vegetation Classification, (Rodwell 1992),

typically occurs on deep, alluvial, moisture-retentive soils of intermediate fertility and productivity. In the UK, the community is predominantly found within four major river catchments; the Thames, Yorkshire Ouse, Trent and Severn. There are currently less than 1500 hectares of these meadows remaining, with 98% lost in the 20th century, and 62% of sites are less than 10ha in size, (JNCC 2007). Current known threats to their distribution include agricultural intensification, inappropriate drainage, and late or missed hay-cuts, (Rodwell 1992; Gowing, Tallowin et al. 2002). Of these, alteration of the hydrological regime and increased availability of nutrients - particularly phosphorus – have been described as the key drivers of change within established meadows, (Gowing 2002; Kennedy, Milne et al. 2003; Toogood and Joyce 2009).

Floodplain meadows are currently the focus of considerable stakeholder investment in the form of various conservation initiatives and agri-environment schemes, (Jefferson 1997). NVC MG4 is listed under Annex 1 of the European Habitats and Species Directive, and both MG4 and its associated communities, MG5 *Cynosurus cristatus* - *Centaurea nigra* grassland and MG8 *Cynosurus cristatus* - *Caltha palustris* grassland, feature within the UK's National and Regional Biodiversity Habitat Action Plans, (http://www.ukbap.org.uk).

1.6 Selected species

Three meadow species were selected for study; *Fritillaria meleagris*, or Snake's Head Fritillary, *Leontodon autumnalis,* or Autumn Hawkbit, and *Rhinanthus minor,* or Yellow rattle. The first is a Nationally Scarce species, the second a constant component of the NVC MG4 community, and the third; a hemi-parasitic species often used as a conservation tool within restoration projects.

The possible occurrence of shifts in hydrological niche within these species can be suggested by plotting their hydrological preference ranges across multiple sites, as has previously been undertaken by the Floodplain Meadow Partnership, (Figure 1). The dark-toned areas of the graphs below display the favoured regime of *Leontodon autumnalis* and *Rhinanthus minor*, with the vertical axis representing the degree of waterlogging the species can tolerate in units of metre weeks, and the horizontal axis showing the degree of soil drying each can support. It is clear that these species display a bimodal distribution in terms of hydrological preference, tolerating both extremely dry ends of the spectrum but also quite moist habitats. As *Rhinanthus* is an annual, the bimodal distribution displayed is not likely to be the result of ontogenetic

factors, and may instead be related to absence of sites containing this species or lack of the preferred range of hydrological data, but further research is required to investigate this.

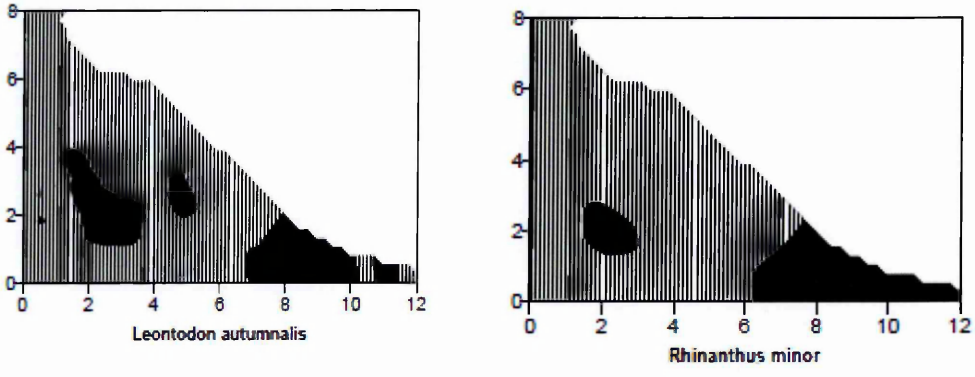


Figure 1.1 Bimodal distributions in hydrological preferences of meadow species, The vertical axis represents the degree of waterlogging the species can tolerate in units of metre weeks, and the horizontal axis, the degree of soil drying each can support, in metre weeks, (Gowing 2002).

1.6.1 *Fritillaria meleagris*

One of NVC MG4's rarer components, *Fritillaria meleagris*, is a long-lived, bulbous geophyte belonging to the *Liliaceae*, and has a moisture indicator value of 8, (Ellenberg 1979). It is known from less than 30 sites in the UK, with 80% of the national resource found on North Meadow NNR in Wiltshire. Germination of fritillary takes place in early spring after a period of stratification, and it spends its first year as a cotyledon. Each

subsequent year the old bulb is renewed and totally replaced by the end of June, and the size of the bulb, (reflecting the quantity of photosynthetic assimilates stored during the growing season), determines the number of leaves produced and whether or not it flowers the following year, (Zhang 1983).

The flowers appear in April, (no earlier than five years after germination), and are pollinated by bees and bumblebees. The plant has two main periods of dormancy; during mid-summer and mid-winter, though the species can also remain below ground altogether or reverse age-state during unfavourable years. Seeds are flat, papery and weakly winged, and approximately 130 are produced per capsule. Fritillary age-states can usefully be classified using the method devised by Barkham, (Barkham 1980), and Zhang, (1983), with the term "age-state" here referring to developmental rather than actual age;

Juveniles = *1 leaf*

Sub-adults = *2 to 3 leaves*

Vegetative adults = *4 to 8 leaves*

Flowering adults = *4 to 8 leaves, plus inflorescence(s).*

1.6.2 *Leontodon autumnalis*

Leontodon autumnalis, or Autumn hawkbit, is a perennial herb belonging to the *Compositae*, with a moisture indicator value of 6. It flowers from June to September, with germination taking place from the autumn through to spring. Its seeds are persistent, and consist of a feathery, wind-born pappus.

1.6.3 *Rhinanthus minor*

Rhinanthus minor or Yellow rattle, is an annual herb belonging to the *Orobanchaceae*, and has a moisture indicator value of 5. It forms hemi-parasitic associations with the roots of a wide range of meadow species, (usually grasses and legumes), and is considered to reduce the vigour of the host plant. Flowering from June to September, *Rhinanthus* requires a period of winter-chilling to germinate the following spring, and it seeds are winged and comparatively robust, but not persistent.

1.7 Study sites

North Meadow in Wiltshire, (GR:SU094946), and Mottey Meadows in Staffordshire, (GR: SJ839132), were selected as key locations for field-experimentation as relatively long-term botanical and hydrological data were available for both sites, and they contain, respectively, the largest and most northerly populations of *Fritillaria meleagris* in the UK.

North Meadow is 109 acres in size, and a designated National Nature Reserve, Site of Special Scientific Interest, and Special Area of Conservation, situated within the glacial floodplain of the River Thames and the River Churn. The soils on North Meadow are typically composed of clay loams overlying a superficial sand and gravel aquifer, and drainage is maintained through a network of grips and ditches, with a primary paleochannel transecting the site. It receives an average rainfall of 651 mm per year, with average January and July temperatures of 3°C and 16.3°C, (www.climate-data.org).

Mottey Meadows is 44 acres in size, and lying within the broad valley of Motteymeadows brook, is also an NNR, SSSI and SAC. Soils consist of peaty loams overlying fluvio-glacial gravels, (the latter thought to form a

superficial aquifer), and the site is drained by a complex system of ditches and underground drains. It receives an average of 690 mm of rainfall per year, and has average January and July temperatures of 3°C and 15.7°C; reflecting its more northerly latitude.

1.8 FMP datasets and hydrological modelling

The Floodplain Meadow Partnership, (FMP), has been compiling botanical and hydrological data derived from site-monitoring for over twenty years; representing the longest dataset for this grassland type in Europe, (Floodplain Meadow Partnership website: www.floodplainmeadows.org, Research zone, - Open University UK, (accessed January 2012)). The botanical data include the results of replicated surveys of eighteen meadow sites around the UK, (including North Meadow, and Mottey Meadows NNRs), in addition to twelve years' of detailed Fritillary-count data collated from 200 replicated plots just from North Meadow. The latter also receives full botanical surveys later in the season; providing the basis for variables such as percentage cover and diversity of fritillary associates, as well as community description according to National Vegetation Classification accounts, (Rodwell 1992).

Water-table depths for survey plots are derived from a site-specific shallow aquifer model, (Gowing and Spoor 1998 ; Gowing 2002), validated by soil-water level data collected from *in situ* data loggers. These loggers are secured in dipwells positioned at various locations around each site, and record the water level every four hours, with data collated annually. Together this system enables water-table depth figures to be accurately determined for all survey plots across each site.

1.9 Aims and objectives

The aims of this study were three-fold. Firstly, it aimed to determine whether ontogenetic niche shifts are occurring along a hydrological gradient within *Fritillaria meleagris*, and other selected meadow species. Secondly, it aimed to quantify the hydrological regime associated with peak numbers of each fritillary age-state and the fritillary population as a whole, and identify the key hydrological periods and response-times of relevance to the study of age-states and species, and lastly, it aimed to assess the underlying mechanisms of flood-related gap dynamics; namely, whether a reduction in flood-sensitive grasses could represent the key factor involved. It is hoped that the results can be of benefit to

conservation-management within floodplain meadows. Within these general aims, the study had the following objectives:

(a) To examine whether ontogenetic niche-shifts can be detected within fritillary and additional species along a hydrological gradient.

(b) To determine if and how response-lags differ between fritillary age-states, and the key lengths and timing of hydrological variables most appropriate with which to study their dynamics.

(c) To investigate whether these niche differences are sufficiently divergent to see corresponding differences in age-state associates and communities.

(d) To examine whether recruitment is enhanced by a treatment simulating the effects of flood within a range of meadow species.

(e) To investigate any correlation between abundance of juvenile fritillaries and reduction in cover of flood-sensitive grasses.

1.10 Study approach

The study involved a field-experiment and also analysis of long-term botanical and hydrological data derived from the Floodplain Meadow Partnership database. Fieldwork consisted of a factorial experiment, examining germination success of meadow species along a hydrological gradient, which had incorporated two levels of competition. Database analysis was undertaken using various techniques to investigate the relationship between species and age-state abundance and hydrological regime. The main experimental section can be found in Chapter 4.

Chapter 2

Fritillary ontogeny and the hydrological gradient

This chapter investigates evidence for the occurrence of ontogenetic niche shifts within the population of Fritillaria meleagris L. *on North Meadow National Nature Reserve, Wiltshire.*

Chapter 2: Fritillary ontogeny and the hydrological gradient

2.1 Introduction

The effective conservation of a particular target species requires an in-depth knowledge of its ecology, and there is a growing body of research to suggest that a fundamental understanding of the ways in which a species niche can change throughout ontogeny is essential to acquiring this, (Parrish and Bazzaz 1985; Quero, Gomez-Aparicio et al. 2008). In comparison to some important agricultural crop species, studies of semi-natural grassland plants involving ontogenetic factors are still comparatively rare, and those derived from long-term field observations, especially so, (Gowing, Tallowin et al. 2002; Bertrand, Gégout et al. 2011).

Amongst the few ecological accounts of native populations of *Fritillaria meleagris* that currently exist, there remains considerable divergence of opinion with regards to its exact requirements, most notably in relation to the timing and relative importance of environmental events, but also in terms of the species' temporal lag in response to these.

No definitive guidelines exist as yet that outline the critical time-scales or types of habitat variables most relevant to the conservation-management of fritillary populations, and it seems probable that the exclusion of ontogenetic factors could at least partially account for this lack of consensus.

2.1.1 The role of flood

The Ellenberg system of ecological classification, derived from extensive habitat association records, gives *Fritillaria meleagris* a value of 8 on the moisture scale, (Ellenberg 1979), but there is growing evidence to suggest that raised water-levels and prolonged waterlogging can be detrimental to some aspect of the long-term survival of this species. One study concluded that waterlogging in spring the year prior to survey accounted for large drops in fritillary numbers, (Zhang 1983), but conversely, another suggested that flooding in summer of the preceding year could also account for a dramatic increase in germination and overall population size documented during its study, (Tatarenko 2013). Many ecologists believe that the flood pulse represents the key driver of spatio-temporal dynamics within floodplain vegetation, (Hughes, Adams et al. 2001; Boudell and Stromberg 2008; Jung, Mony et al. 2009; Raulings, Morris et al. 2010), but others have claimed that *Fritillaria meleagris* has no actual ecological

dependence on flooding at all, and that additional factors such as withdrawal of traditional management practices may pose a greater risk to its distribution. Similar assertions have been made elsewhere regarding its associated Great Burnet Community, (listed as NVC MG4 within the National Vegetation Classification, (Rodwell 1992), where altered nutrient relations following sediment deposition has been cited as of possible greater relevance to community persistence than changes in hydrology *per se,* (Gowing, Tallowin et al. 2002). It is clear that interpretation of the role played by flood and the significance of its timing in relation to fritillary numbers has varied widely and that additional clarification is required, particularly in relation to ontogeny.

The minimum elevation limits of floodplain plants have frequently been interpreted to represent their degree of tolerance to flooding, (van Eck, van de Steeg et al. 2004), and preliminary analysis of the fritillary dataset, (derived from annual repeat surveys from 1999-20012, and undertaken by research staff within the Open University and the Floodplain Meadow Partnership), has also found elevation to represent a useful proxy in relation to fritillary presence and absence patterns on North Meadow, (Tatarenko 2013).

A general shift of fritillary to higher elevations following a rise in the elevation of the water-table due to modifications of the nearby river system between 1940 and 1981 has also been documented by Zhang in Sweden, (Zhang and Hytteborn 1985). Zhang further pointed to a difference in the spatial locations of age-state distributions in relation to water-regime during his study; with a greater proportion of juveniles apparently recorded from moderately wet sites and flowering adults more associated with moderately dry locations, although he did not examine these patterns directly in relation to elevation, and long-term, continuous data were not available for his research. It remains unknown whether elevation could serve as a useful proxy for differential waterlogging tolerances between age-states, and whether niche-shifts can be in fact detected on this basis.

2.1.2 Sum exceedence values and age-state dynamics

It is questionable whether the methods applied for the analysis of community changes are equally appropriate for studies of age-state behaviours, and the differing types, lengths and time-scales of hydrological and botanical data employed by some studies, (especially the

absence of ontogenetic considerations characteristic of most), may have also contributed to the contrasting interpretations of overall fritillary population dynamics.

The principle of Sum Exceedence values, (Sieben 1965), outlined in Chapter 1, has been successfully applied to monitor NVC MG4 response to altered hydrology on UK floodplains, (Gowing 2002), and also to assess patterns of whole-species niche-segregation along hydrological gradients in the Fynbos, (Silvertown, Dodd et al. 1999; Araya, Silvertown et al. 2011), and is now becoming a standard tool within meadow conservation, but the method could also have its limitations in relation to certain applications.

SEVs are usually derived from five year rolling averages in water-table depth, which has been identified as the most appropriate grain with which to analyse between-site meadow-community distributions. However, some express the view that this approximation does not fully take into account the seasonal timing and within-season fluctuation-range of the water-regime, variables which have been identified as of primary significance to floodplain vegetation, (Grevilliot, Broyer et al. 1998), and which seem likely to be of particular relevance also to ontogenetic niche

shifts within species, (Parrish and Bazzaz 1985; Nakashizuka 2001; Penuelas, Terradas et al. 2011).

Sum Exceedence Values derived from five year averages have been applied to classify *Fritillaria meleagris*, (where general tolerance ranges of between 10 and 20 weeks per year of "wet" and "dry" soil moisture levels have been assigned), with the inherent assumption that time-scales shorter than five years are of minor significance to species dynamics. It has been admitted, however, that the Sum Exceedence Values assigned to species may not be entirely representative; that as many species occur in several community-types their ranges might not be as tightly defined as those of communities, (Gowing, Tallowin et al. 2002). It seems more likely, however, that the reverse could be true. The tolerance ranges of individual age-states could in fact be more specific than, or at least differ from, those of both the species as a whole and those of the multi-species community to which it belongs, and the temporal lag in age-state response to environmental conditions could well be shorter than five-years, certainly in relation to juveniles.

On the supposition that response-lag is age-state-specific, and that the most appropriate length of hydrological variables will vary according to

floristic measure, time-series analysis including the incorporation of seasonal hydrological variables of short as well as long duration could therefore be of greater relevance to the study of age-state dynamics than five year averages alone. It is clear that further work is required to establish whether ontogenetic niche shifts are definitively occurring within the Fritillary population on North Meadow, and to identify both the nature and time-scale of environmental variables that could best explain such differences in distribution, and this has given rise to the following hypotheses:

2.1.3 Hypotheses to be tested:

(a) Ontogenetic niche shifts occur along a hydrological gradient within the fritillary population in North Meadow NNR

(b) Flooding promotes recruitment from seed within the fritillary population.

(c) The response-lag of fritillary age-states and the length of hydrological periods of key relevance to their distribution are shorter and more seasonally-dependent than for the species as a whole.

The following study provides an ideal opportunity to investigate the phenomena of niche-shifts through ontogeny and the environmental parameters most associated with optimum population abundance. It is hoped that results will be of interest to conservation practitioners and lead to further related research of Fritillary and other floodplain meadow species.

2.2 Methods

2.2.1 The datasets

Two primary botanical and hydrological datasets were variously formatted within SPSS, Canoco and Excel to investigate the hypotheses described above.

(a) With floristic data derived from repeat annual surveys, (outlined in Chapter 1), counts of the four primary age-states were calculated for each of the 120 quadrats within Block 1 at Cricklade, for the period 1999 to 2008, following the classification method devised by Barkham, (1980).

(b) Fortnightly modelled estimates of water-table depth at each sampled location, derived from the dipwell monitoring and hydrological model outlined in the previous chapter, were extracted and calculated by season, (i.e., spring, summer, whole growing season and winter), with values averaged across the whole of Block 1. Temporal lags of 0 to 3 years were assigned to each, (i.e. with each value given the form of year-t, t-1, t-2, t-3, etc.).

(c) Annual and whole growing season hydrological data for one-, two-, three-, four- and five-year rolling averages for the years (1996-) 1999 to 2008, were subsequently extracted to produce the following more detailed quadrat variables listed below. These variables were calculated for each of the annual and growing season run-lengths, and temporal lags of 0 to 3 years were assigned to each, (i.e. with each annual or growing season value given the form of year-t, t-1, t-2, t-3, etc.).

- mean water-table depth
- median water-table depth
- interquartile range in water-table depth
- standard deviation in water-table depth

- the duration and extent that the water-table surpasses the drought threshold
- the duration and extent that the water-table surpasses the flooding threshold
- the sum exceedence values for both drought and flood

(d) Water-table depth estimates were then averaged by season, (i.e., spring, summer, whole growing season and winter), to produce the same range of quadrat hydrological variables as listed above, and these were also classified according to temporal lags of 0 to 3 years, (i.e. with each seasonal hydrological value given the form of year-t, t-1, t-2, t-3, etc.).

(e) Botanical and environmental datasets encompassing the above were created in Canoco for the purposes of Correspondence Analysis, (Ter Braak 1987), and bar charts, heat and scatter graphs, were created in Excel.

2.2.2 Elevation as a proxy for waterlogging

To assess the effectiveness of using elevation as a proxy for general waterlogging tolerances, and to investigate whether niche-shifts could be detected on the basis of this proxy, linear regression was first undertaken within SPSS. The mean, median, mode, minimum and lower quartile quadrat-elevations of the age-state groups were then compared.

2.2.3 Time-series analysis

Preliminary time-series analysis was carried out to detect key lags in response-time and to examine whether individual age-state abundances were associated with particular seasons. Multiple regressions were performed in SPSS, involving total annual counts of age-states as the dependent variables and seasonal water-table depths averaged by year over the block, and formatted to include time-lags of 0 to three years prior survey, as the explanatory variables. Significant results were then corrected for multiple comparisons, using False Discovery Rate Analysis, (Benjamini 1995), and displayed in graph-form.

2.2.4 Hydrology and age-state dynamics

In the search for the hydrological variables of most significance to age-state numbers, stepwise multiple, forwards and forced entry regressions were undertaken in SPSS for each of the detailed hydrological datasets, i.e. which included both annual, growing season and seasonal data. The most significant hydrological variables resulting from each age-state analysis within each dataset, (selected on the basis of their P and Adjusted R^2), were subsequently combined into a final one, (resulting in a total of twenty potentially significant hydrological predictor values). Forced entry, forwards and multiple regression were carried out to identify the most relevant of these. Data for the key variables were transformed using the equation Log(n+1) and corresponding scatter graphs produced in excel.

Subsequent stepwise multiple regressions were also undertaken, including combinations of year and quadrat with the hydrological variables listed above as predictor variables. However these models were eventually deemed unsound statistically and not dealt with further.

Canonical correspondence analysis biplots were created to display the relationships between age-states and their hydrological correlates, for both the full ten year period, and also for 2008 alone. The latter was

undertaken to investigate whether the relationships could be seen to differ significantly once the possible effects of temporal and spatial autocorrelation had been removed.

CCA analyses focused on interspecies distances without transformation or downweighting, with variable selection entered manually, and the subsequent results were tested using the Monte Carlo test, with 499 permutations.

2.2.5 Hydrology and population optima

Similar methods applied to age-state analysis were applied to investigate the key hydrological variables associated with total population abundance, though with total fritillary counts entered as the dependent variable. Graphs were subsequently produced to display the response of the population as a whole and also each of the age-states to the selected variable.

2.3 Results

2.3.1 General population and age-state trends

Preliminary schematic heat maps displaying quadrat elevation and total fritillary counts, (Figures 2.1 & 2.2), demonstrate the clustering of fritillary in higher locations and absence from the lower sites associated with the paleochannel that runs through Cricklade, (coloured dark blue).

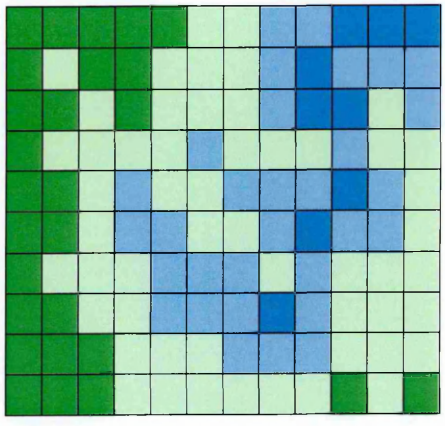


Figure 2.1 Quadrat elevation

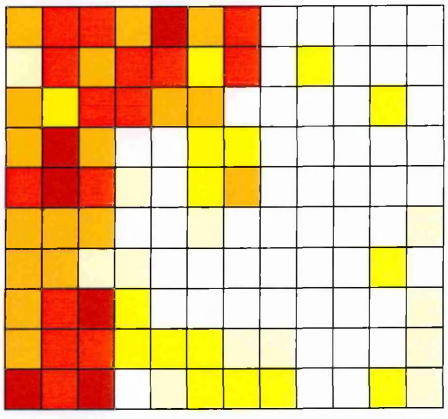


Figure 2.2 Total fritillary counts

= 78.1 to78.39m = 78.4 to 78.59m = 1 to 5 = 6 to 20

= 78.6 to 78.79m = 78.8 to 78.99m = 21 to 50 = 51 to 150

= 151 to 230 (fritillaries)

Figures 2.1 & 2.2 The heat maps display, schematically, the 120 x 1m² quadrats of Block 1; together representing a total area of approximately 4 ha, (200m x 200m).

The bar charts highlight the substantial between-year fluctuations in terms of both numbers, (Figure 2.3), and spatial location, (Figure 2.4), of age-states during the period. It seems that there has been a general increase in the overall population of fritillary since 2001 in response to the favourable influence of some key parameter.

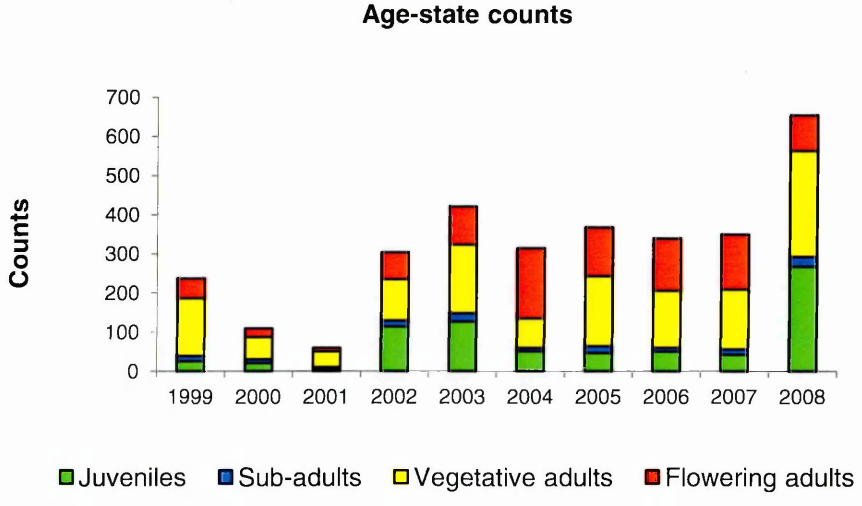


Figure 2.3 Age-state counts per year (1999 to 2008)

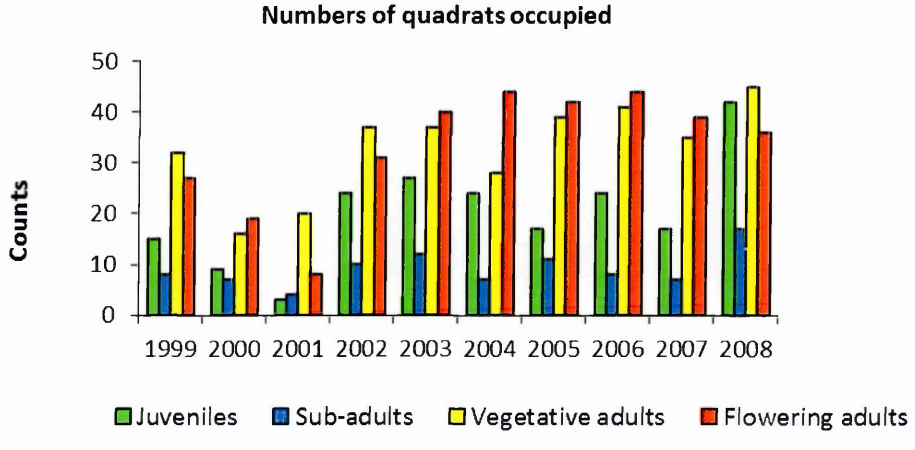


Figure 2.4 Age-state quadrat occupancy by year (1999 to 2008)

The greatest changes in total fritillary counts was seen in 2002, and 2008, both of which followed very wet years, and were associated with very large increases in the size of the juvenile population. The juveniles also displayed a marked drop in numbers between 2003 and 2007, thought to be attributable to the high mortality rate of this group in comparison to adults, (Zhang and Hytteborn 1985; Tatarenko 2013).

The numbers of sub-adults steadily increased after 2001, (a pattern considered to reflect the stability of the Fritillary population as a whole within Cricklade), and the marked fluctuation amongst numbers of vegetative adults over the period in question is thought to be indicative of the frequent occurrence of age-state reversal, (i.e. of transformation from the flowering state to the vegetative one, and vice-versa); which is a common feature of polycarpic perennials. Numbers of flowering adults peaked during 2004, known to be a particularly dry year.

These exploratory investigations confirm the probable relationship between juvenile germination peaks and some element of flooding the preceding year, in addition to a possible link between flowering individuals and drier conditions.

2.3.2 Elevation as a proxy for waterlogging

The results of linear regression confirmed the significant relationship between elevation and the distribution of both individual age-states and the Fritillary population as a whole, although the low R^2 adjusted values amongst all groups indicate that a large degree of their variation about the mean cannot be explained by the models, (Table 2.1).

Included terms	F	B	t	R^2adj	P
i. Juveniles	112.258	3.99	10.6	0.09	<0.01
ii. Sub-adults	92.113	0.82	9.6	0.07	<0.01
iii. Vegetative adults	245.468	0.41	15.67	0.17	<0.01
iv. Flowering adults	240.243	4.57	15.5	0.17	<0.01
v. Total Fritillaries	298.521	16.47	17.28	0.02	<0.01

Table 2.1 Summary of enter regressions between age-states and elevation.

The heat map, (Figure 2.5), identifying the quadrat-elevations where juveniles and flowering adults had never been recorded, but other age-states had, (marked J and F, respectively), suggested that juveniles may be less frequent at lower, wetter, locations than flowering adults at this site, in contrast to the findings of Zhang, (1983).

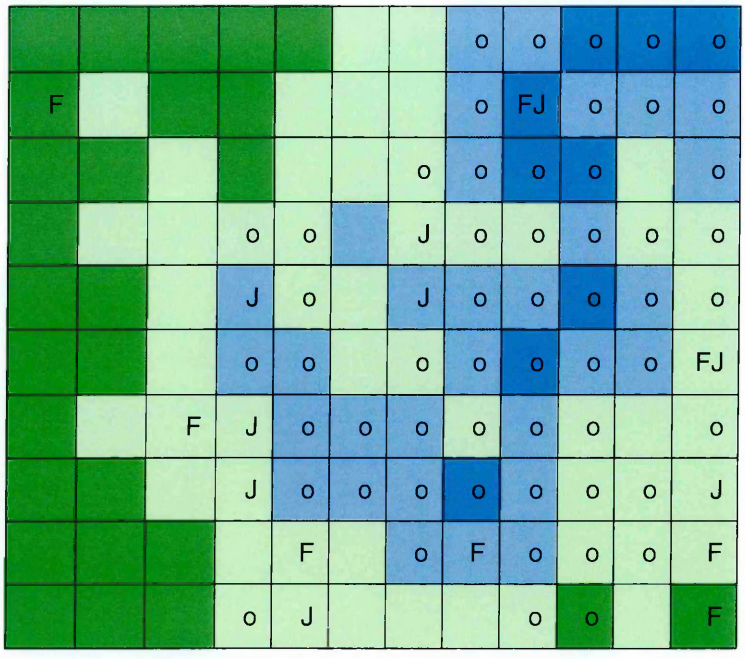


Figure 2.5 Quadrats occupied by fritillary where flowering adults, (F), and Juveniles, (J), are never recorded, despite availability of apparently suitable habitats. (Quadrats marked "0" represent those where fritillaries have never been recorded, those with no lettering indicate the recording of one or more age-states at some point).

Subsequent comparisons of quadrat-elevations for the period 1999 to 2008, revealed, however, that both the medians and modes were identical for all groups, (at c. 78.8m). Some differences were detected in relation to minimum elevation, (Figure 2.6), which differed between juveniles and flowering adults by approximately 10cm, and also to a lesser extent for lower interquartile range in elevation, where they differed by about 1cm. However, only a handful of quadrats showed these low minimum

elevation values, and clearly no substantial ecological inference could be made in relation to a 1cm difference in lower interquartile range.

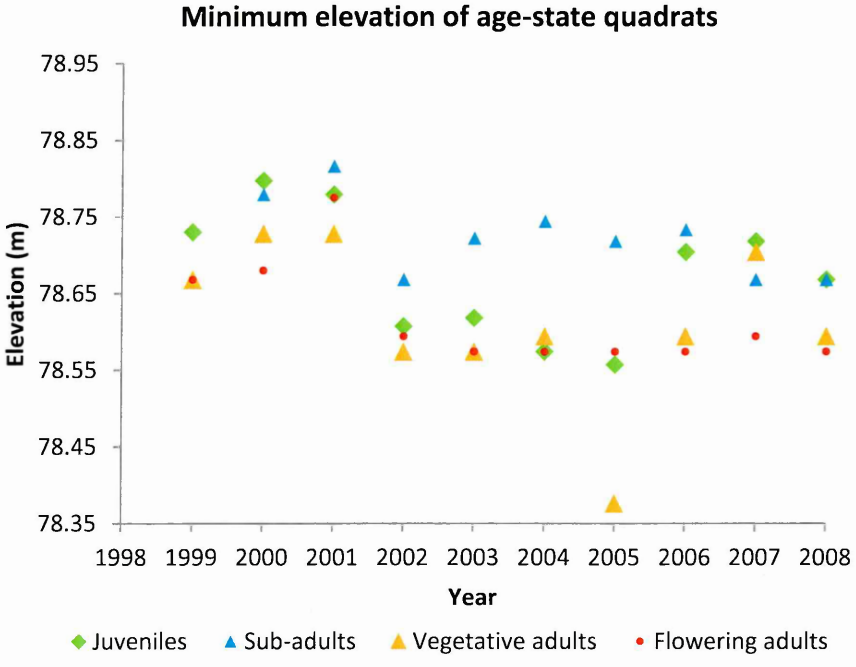


Figure 2.6 Age-state minimum elevations

Therefore, although the contrast in trend between the groups was quite consistent, the identical medians and modes meant that overall the actual difference between groups was minimal, and establishing niche-shifts on the basis of minimum elevation as a proxy for waterlogging tolerance would not appear to be justified.

Although elevation is evidently not the key spatial differentiator, investigation of quadrat co-occurrence indicates that age-states do display quite different physical distributions. Of the total 438 recorded samples of

juveniles and flowering adults between 1999 and 2008, they were found together in only 35% of quadrats, with 65% occurring in separate localities, (Figure 2.7). Subsequent analysis confirmed that the frequencies with which juveniles and flowering adults occur together are less than one would expect by chance, and that the occasions they occur apart are more frequent, (x^2= 38.5, and P = <0.01).

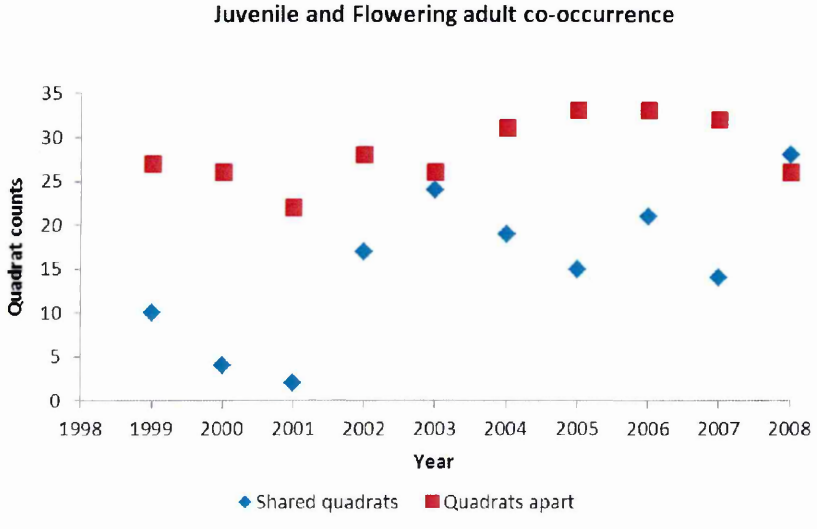


Figure 2.7 Age-state co-occurrence patterns

The frequency that juveniles and flowering adults were found in different quadrats remained consistently high throughout the period, and major changes were seen only in the numbers of instances that they were recorded together. Numbers of these dipped in 2001, as did the population as a whole, and the greatest changes in co-occurrence were seen in the increases of 2002 and 2008, both representing peak

germination events following flood. As they are less likely to be found together as development progresses, these results might indicate that the niche requirements become narrower, supporting the findings of other ontogenetic research, (Eriksson 2002; Quero, Gomez-Aparicio et al. 2008), although it might simply be that niche-contraction represents a general function of higher juvenile versus flowering adult numbers, in this case.

2.3.3 Time-series analysis

Preliminary results of regressions between age-state counts and seasonal water-table depth averages over the ten year period, revealed a significant positive correlation between the numbers of flowering adults and drier conditions during spring of the year prior to survey, (Figures 2.8 and 2.9).

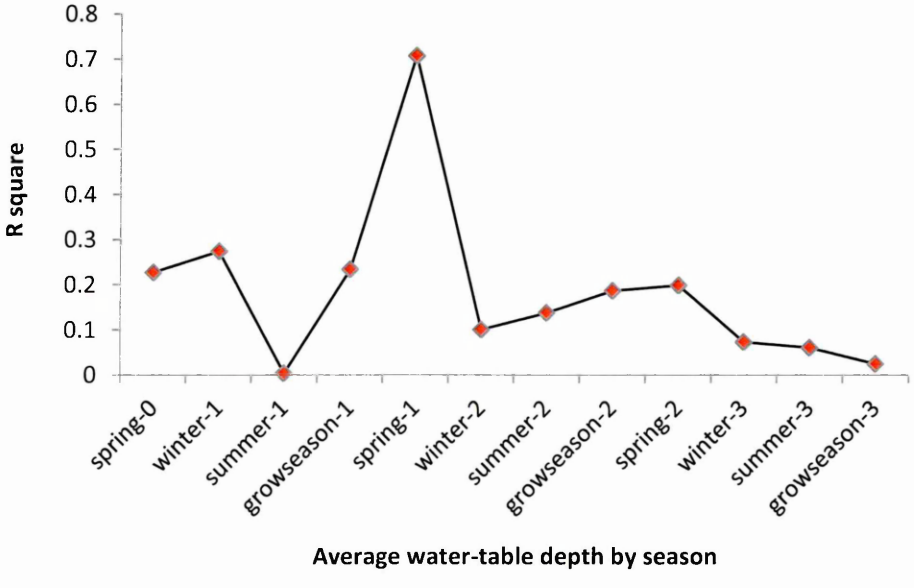


Figure 2.8 Time-series analysis and degree of R^2 correlation following regression between numbers of flowering adults and average-water-table depth by season, 0-3 years prior to survey (1999-2008).

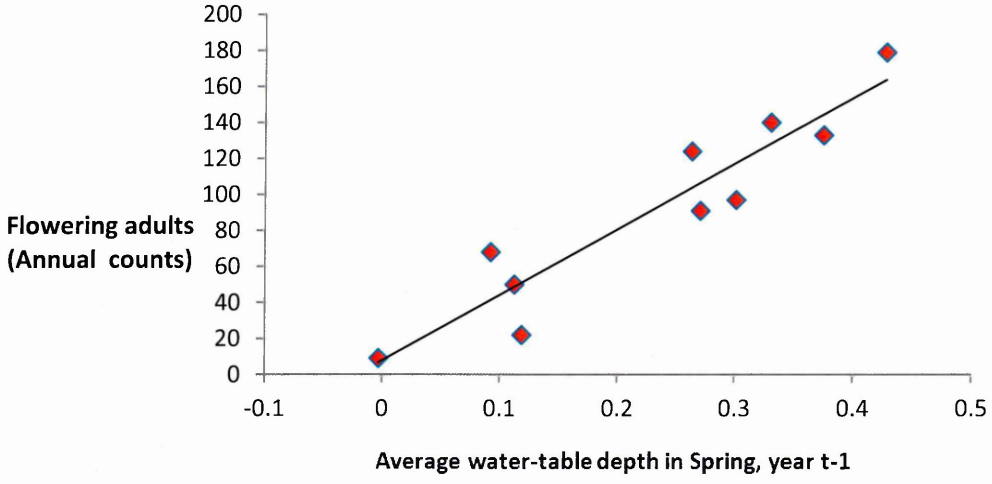


Figure 2.9 Scatter graph displaying the significant relationship between numbers of flowering adults and mean water-table depth during spring of the year prior to survey; with $R^2 = 0.7069$ and $P = 0.00365$, using False Discovery Rate Analysis of the 12 hydro-season variables.

Although results of these analyses, using water-table depths averaged across the block, (n= 10), were significant only for flowering adults, this group was indeed found to be associated with a short temporal response-lag, confirming that the inclusion of shorter term, seasonal hydrology within analyses of ontogenetic niche shifts would be appropriate.

2.3.4 Hydrology and age-states

Subsequent regression analysis involving the full hydrological variable dataset, (i.e. including seasonal and SEV values), revealed a high degree of correlation between several of the hydrological variables, and the differences in Adjusted R^2 between those selected and those discarded were very minor, in some cases, (Table 2.2). Surprisingly, the best-fit hydrological models were seen to account for much less of the variation about the mean than the results of the preliminary time-series analysis, (Figure 2.9); a pattern thought to be due perhaps to the higher data values associated with block counts versus quadrat counts. Overall, however, the results did highlight a significant contrast in age-state- environmental relations, in terms of both the facet of the water-regime associated with peak numbers of each, and the timing of such events, and consequently confirm the hypothesis that ontogenetic niche shifts are occurring within North Meadow populations of fritillary.

Included terms	B	t	R^2adj	P
i. Dependent = Juveniles (F = 86.424, df = 1,198, P<0.001)				
Interquartile range in water-table depth, Spring, yr: t-1	0.004	9.29	0.07	<0.01
ii. Dependent = Sub-adults (F = 35.240, df = 1,198, P<0.001)				
Sum Exceedence values for drought, Summer, yr: t-2	0.083	5.94	0.03	<0.01
iii. Dependent = Vegetative adults (F = 107.896, df = 1,198, P<0.001)				
Exceedence above aeration threshold, Annual: 5 yr. av.	-0.013	-10.4	0.08	<0.01
iv. Dependent = Flowering adults (F = 204.354, df = 1,198, P<0.001)				
Duration below drought threshold, Spring, yr: t-1	0.08	14.3	0.15	<0.01
v. Dependent = Total Fritillaries (F = 126.246, df = 1,198, P<0.001)				
Duration above aeration threshold, Annual: 3 yr.av.	-0.006	-11.2	0.09	<0.01

Table 2.2 Summary of enter regressions between age-states and key hydrological variables, selected from stepwise models, using Log (n+1) transformed data. The table gives the overall model fit and the parameter estimates for included terms, in addition to the hydrological variable returning the highest R^2adj.

Key hydrological variables were selected from stepwise regression on the following: Interquartile range in water-table depth, Spring: yr. t-1, (2) Duration below drought-stress threshold, Spring, yr: t-1, (3) Sum Exceedence values for drought, Summer, yr: t-2, (4) Sum Exceedence values for aeration stress, Winter, yr: t-2, (5) Median water-table depth, Annual: 1 yr.av., (6) Exceedence above aeration-stress threshold, Growing season:1 yr.av., (7) Average water-table depth, Growing season:1 yr.av., (8) Median water-table depth, Annual: 2 yr.av., (9) Duration above aeration-stress threshold, Annual: 2 yr.av., (10) Duration below drought-stress threshold, Growing season: 2 yr.av., (11) Duration above aeration-stress threshold, Annual:3 yr. av., (12) Exceedence below drought-stress threshold, Growing season:3 yr.av., (13) Duration below drought-stress threshold, Growing season: 3 yr.av., (14) Duration above aeration-stress threshold, Growing season: 4 yr. av., (15) Exceedence below drought-stress threshold, Annual, 4 yr. av., (16) Exceedence above aeration-stress threshold, Annual, 4 yr. av., (17) Duration below drought-stress threshold, Annual: 4 yr.av., (18) Exceedence above aeration-stress threshold, Annual: 5 yr.av., (19) Exceedence below drought-stress threshold, Growing season: 5 yr.av.,(20) Duration below drought-stress threshold, Growing season: 5 yr.av.

Results of regression pointed to a significant relationship between juveniles and interquartile range in water-table depth, in Spring, the year

prior to survey, i.e. that juvenile abundance would seem to be correlated with quadrat locations that had experienced a greater range in both flood and drought values prior to parental seed dispersal, (Table 2.2). Juvenile numbers peaked around the 0.3 value and exhibited a positive relationship to interquartile range, whereas flowering adults peaked at below 0.1 and were negatively correlated. Figures 2.10 and 2.11 highlight this contrast.

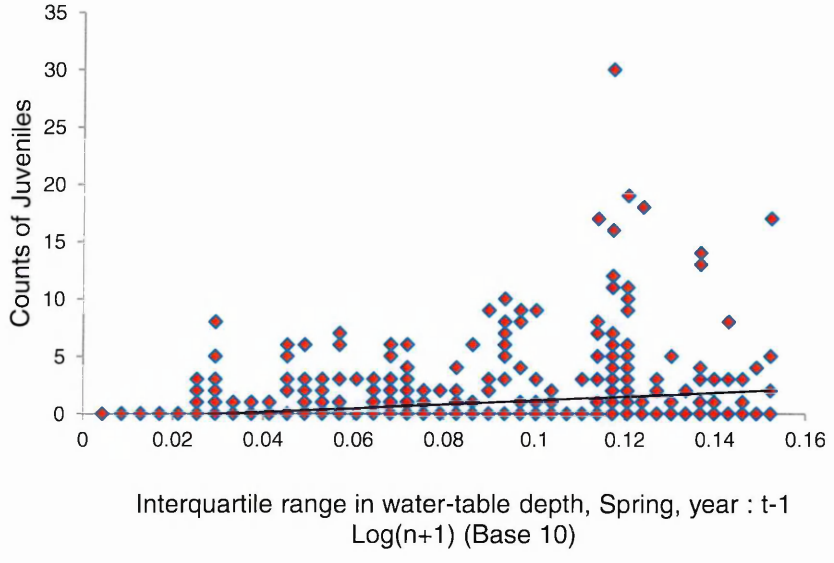


Figure 2.10 Scatter graph using a linear trend line, displaying the relationship between numbers of juveniles and interquartile range in water-table depth during spring of the year prior to survey. The model gave the following equation; : y = 17.023x + - 0.05466, with R^2 = 0.07

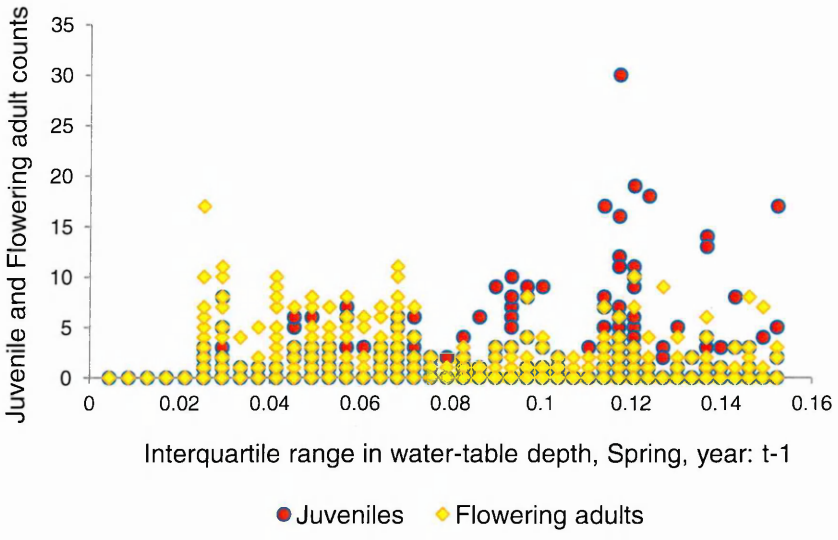


Figure 2.11 Scatter graph displaying the contrast in relationship between numbers of juveniles and flowering adults and interquartile range in water-table depth during Spring of the year prior to survey, using Log(n+1) transformed data.

The most significant variable associated with sub-adults was the sum exceedence value for drought, in summer, two years prior to survey. Zhang notes that the transformation between the juvenile and sub-adult stage often takes longer than a year, (Zhang 1983), and so the relationship between sub-adults and drought two years prior to survey seems likely to refer to the conditions associated with plants during the juvenile stage. Interestingly, the second most significant variable associated with sub-adults during regressions, (not reported in full here), was the Interquartile range in water-table depth, pointing to a gradual shift with age from a niche requiring both flooding and drought prior to parental seed dispersal, to one requiring predominantly drier conditions post-germination. Vegetative adults were negatively correlated with

exceedence above the aeration threshold, (i.e. flood severity), averaged over the previous five years, i.e. suggesting that in the absence of major floods over their recent life-cycle, most were able to reach maturity.

Regression results for flowering adults and the full hydrological dataset matched those of the time-series analysis using water-table depth values averaged across the block, (Figures 2.8 & 2.9), in that they were found to be most closely associated with long periods of drought in spring, the year prior to survey. Optimum frequency of flowering adults was associated with eleven days of drought versus three days for juveniles. As outlined in chapter 1, the capacity to develop a flower bud is determined at some stage during the previous growing season, and these results suggest that the hormonal changes leading to bud-formation could be triggered by conditions in spring of the year prior to survey. Figures 2.12 and 2.13 display the contrast in juvenile and flowering adult numbers in relation to drought, in spring, year: t-1. The results of this study suggest that both the length and timing of the significant hydroperiods can vary considerably between age-states, according to both developmental stage and key events within a species' life-cycle.

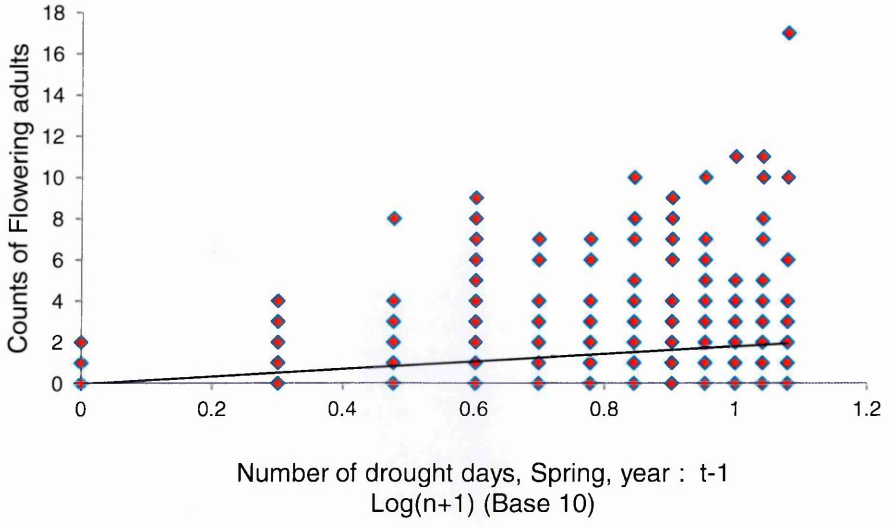


Figure 2.12 Scatter graph displaying the relationship between numbers of flowering adults and drought days during Spring of the year prior to survey, using Log (n+1) transformed data. The linear trendline used the following equation: $y = 1.8286x - 0.0429$, with $R^2 = 0.1457$

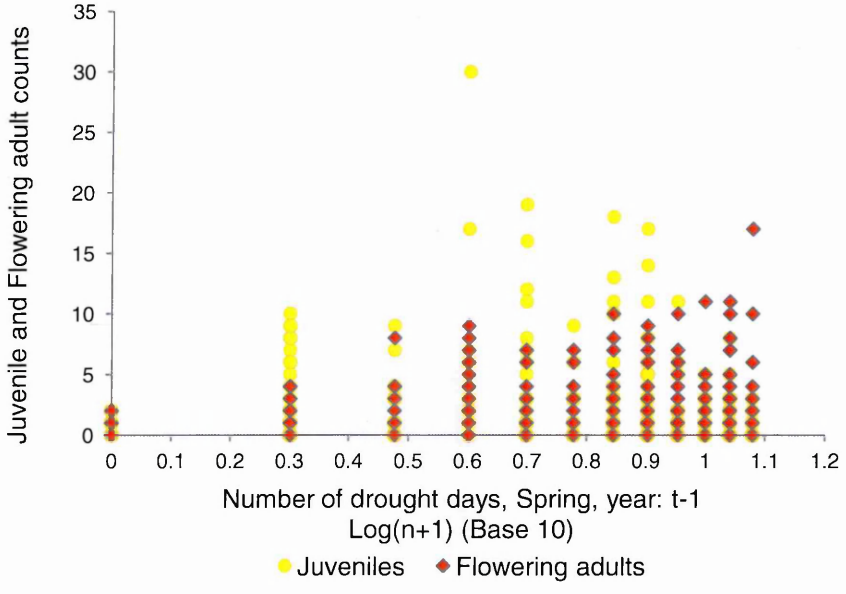


Figure 2.13 Scatter graph displaying the contrast in relationship between numbers of juveniles and flowering adults and drought days during Spring of the year prior to survey.

The CCA biplots display the age-state positions in ecological space in relation to the four hydrological variables selected from the results of

multiple regression, (Figure 2.14). Axis one clearly represents a moisture gradient, with flood severity and interquartile range in water-table depth on the left, and drought duration and sum exceedence values for drought on the right, and in total both axes accounted for c. 86% of age-state-hydrology correlations. Major differences can be seen between the diametrically opposed positions of juveniles and flowering adults, whereas the sub-adults and vegetative adults display a more intermediate position in relation to each other along the axis.

Although the axes are reversed, the CCA biplot produced for 2008 alone displays a similar relationship between the age-states, with juveniles close to the flooding and interquartile range vectors, flowering adults situated on the opposite, drier side of the axis, and sub-adults and vegetative adults holding the intermediate position, (Figures 2.15). These results suggest that the effects of repeat sampling did not significantly alter results, and that the associations between the age-states are consistent between years.

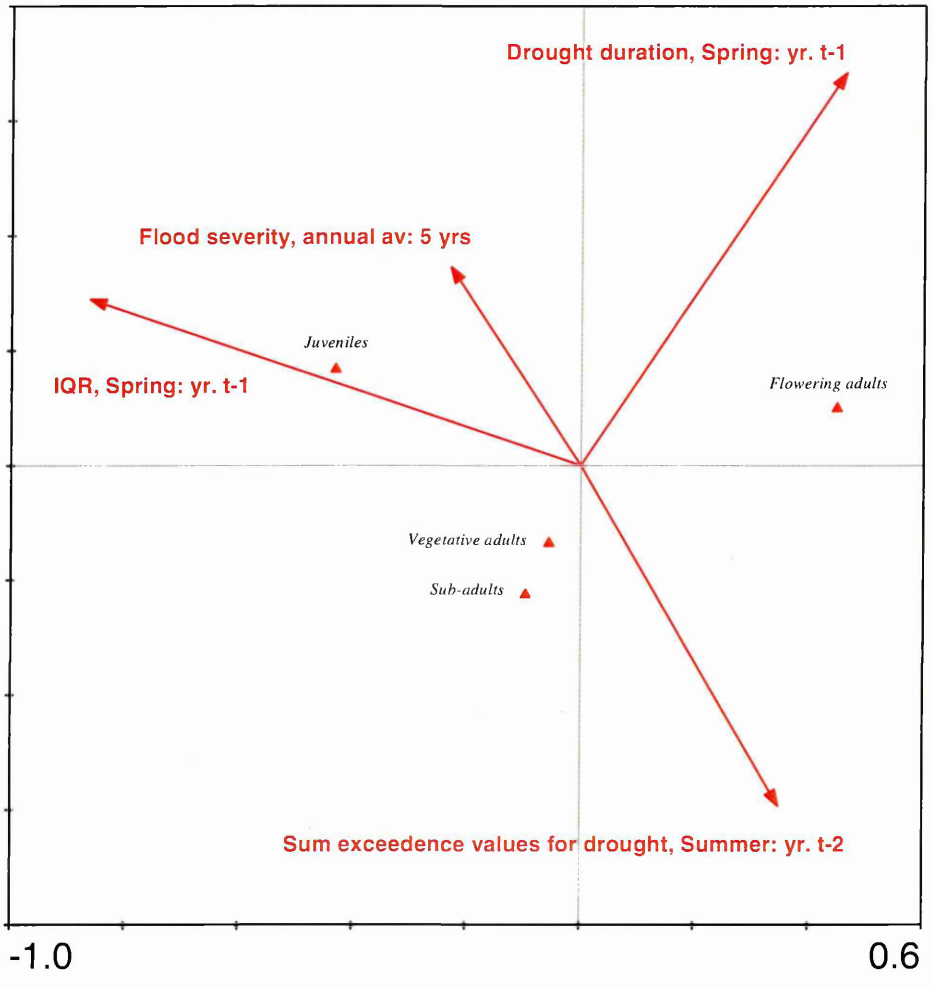


Figure 2.14 CCA biplot of age-state associations with hydrology.

	Axis 1	Axis 2	Total inertia
Eigen value	0.094	0.019	0.662
Age-state-environment correlations	0.549	0.312	
Cumulative % variance of age-state data	14.3	17.2	
Cumulative % variance of age-state-environment relation	82.2	99.0	
Sum of all eigenvalues			0.662
Sum of all canonical eigenvalues			0.115

Table 2.3 CCA correlations

Monte Carlo test	Eigenvalue/Trace	F-ratio	P-value
Significance of 1st canonical axis:	0.09	72.07	0.002
Significance of all canonical axes:	0.12	22.74	0.002

Table 2.4 Monte Carlo test results

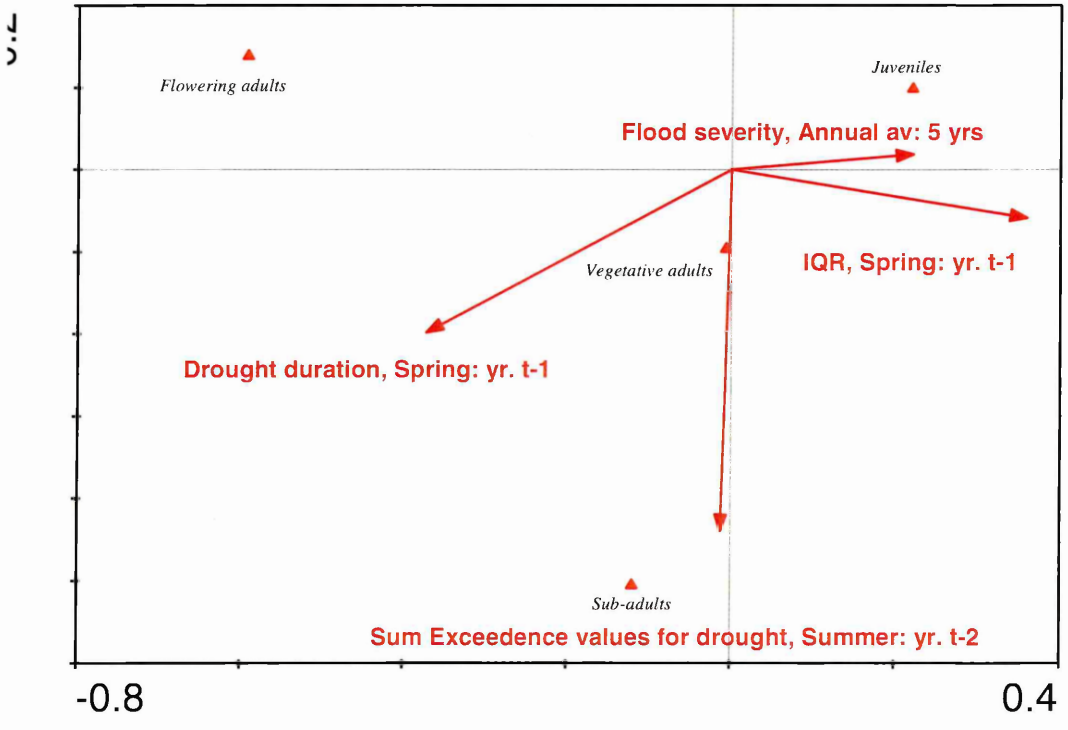


Figure 2.15 CCA analyses of the age-state and hydrology in 2008

2.3.5 Hydrology and population optima

Results from regressions demonstrate that quadrat counts of fritillaries were negatively correlated with flood duration over a three year period, (Figures 2.16and 2.17). 73% of the population occurred in quadrats subject to between 17 and 25 flood days per year, and total site-counts of all age-states reaching a peak at between 17 and 20 days of flood per year.

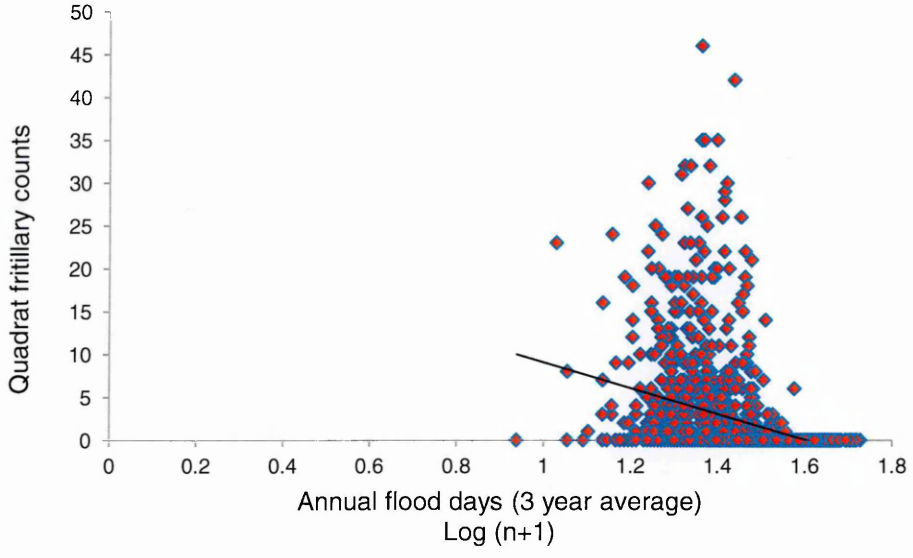


Figure 2.16 Scatter graph displaying the relationship between total fritillary counts and annual flood days, over the preceding three years, using Log (n+1) transformed data. The linear trendline gave the following equation: $y = -15.048x + 24.14$, with $R^2 = 0.1$

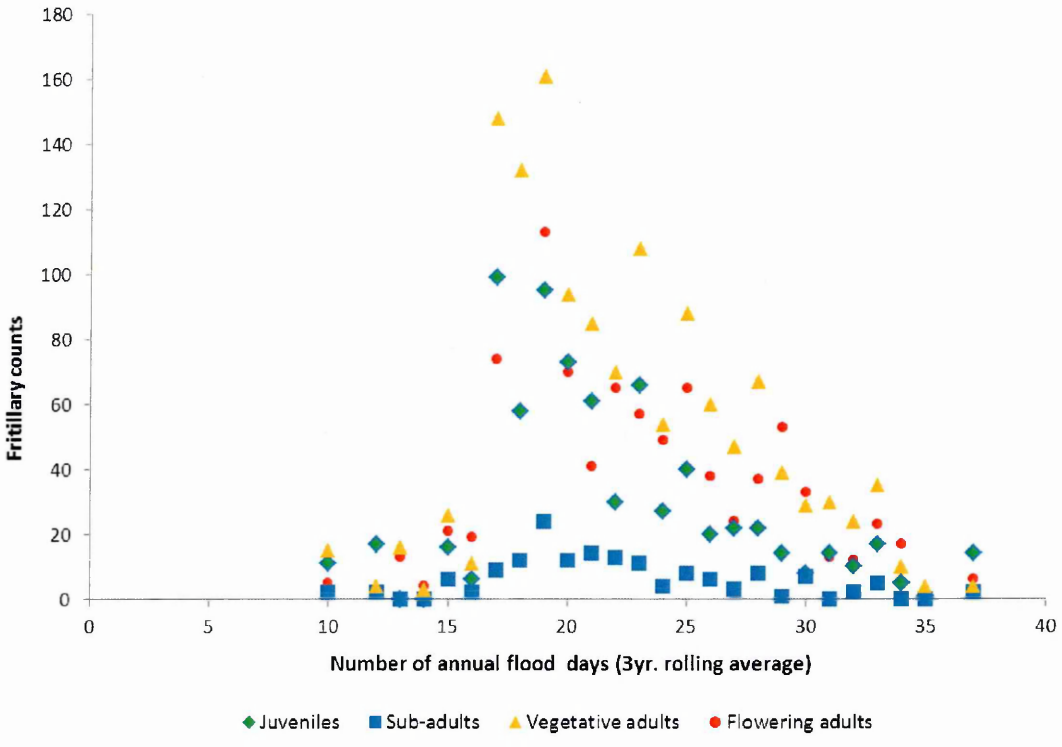


Figure 2.17 Scatter graph displaying the relationship between total age-state counts and numbers of flood days over the preceding three years.

2.3.6 Additional questions

When total fritillary counts and number of annual flood days recorded in 2008 were plotted in heat maps, (Figures 2.18 & 2.19), it became clear that the species was notably sparse or absent from many apparently ideal habitats, and unexpectedly frequent in quadrats one might have thought were unsuitable. This pattern was also seen in the flowering adult/juvenile absence map, (Figure 2.5). For example, in Figure 2.19, one can see that the bottom half of the final column contained many quadrats with

minimal annual flooding, though the same cells in Figure 2.18 displayed very few fritillaries.

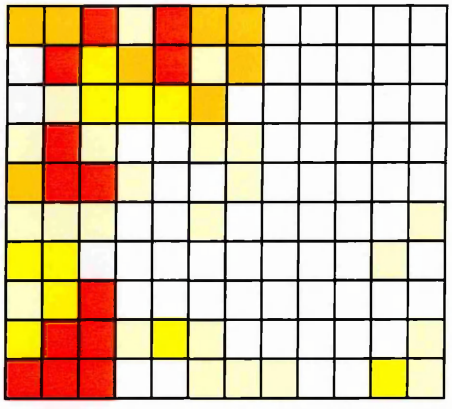


Figure 2.18 Fritillary counts (2008)

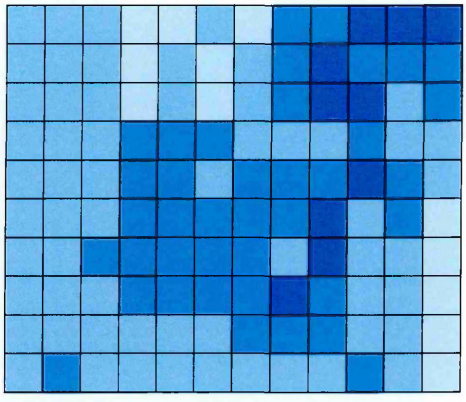


Figure 2.19 Annual flood days (2008)

= 1 to 5
= 6 to 10
= 11 to 20
= 21 to 45

= 15 to 20
= 21 to 30
= 31 to 40
= 41 to 50

Subsequent scatter graphs of the key hydrological variables versus elevation displayed, as one might expect, the general trend of fewer flood days and more drought days as the gradient increased, (Figure 2.19). There was also a corresponding rise in Interquartile range in water-table depth with elevation; a trend characteristic of mid-field sites equidistant to the surrounding rivers. However, the hydrological values reveal a considerable amount of variation that appears to be largely independent of elevation, with variation in these values also reaching a peak at the 78.8m mark associated with the mode and median elevations of all age-state distributions.

These results, combined with the low Adjusted R^2 of the previous hydrological and elevation regressions, (Tables 2.1 & 2.2), suggest that variation in a factor not directly related to either hydrology or elevation could explain further differences in age-state distribution, though these were not explored directly in this study, (see Discussion).

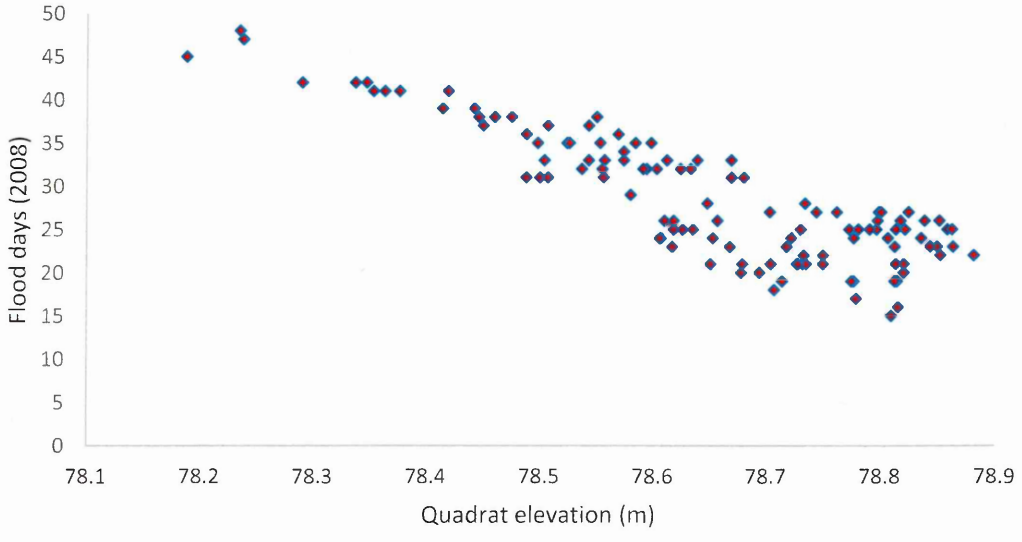


Figure 2.20 Scatter graph displaying the variation in numbers of flood days in relation to quadrat elevation, (2008).

2.4 Discussion

The study set out with three primary aims; (a) to determine whether ontogenetic niche shifts occur along a hydrological gradient within the fritillary population on North Meadow NNR, (b) to investigate whether flooding could be seen to promote recruitment from seed, and, (c), to

identify the length and duration of hydrological variables of most relevance to age-state dynamics; the latter hypothesis being that response-lags would be shorter than for whole species, and involve seasonal rather than annual hydrological variables. Despite certain difficulties and constraints arising from the nature and type of data employed, the study was largely successful in confirming these hypotheses.

Niche shifts were established especially in relation to the pre- and post-seed dispersal stages of fritillary, which differed significantly in terms of hydrological association, (Table 2.2 & Figure 2.12), and were also inferred by the significant contrast in spatial distribution between juveniles and flowering adults, (Figures 2.5, & 2.7). Barrett found a seed-to-seedling shift in patterns of distribution in her research of *Trifolium repens*, (Barett 1992), but in a heathland study of *Vaccinium* species, evidence of shifts was found only between young and mature individuals, (Eriksson 2002). It seems likely that the developmental age at which shifts occur can be species-specific and possibly also be related to habitat-type and the prevailing disturbance-regime.

The association of juveniles with both flood and drought prior to parental seed dispersal could be attributable to a wide range of factors not directly examined by this research, and the close correlation of several of the hydrological variables and their low R^2 values during regressions make the assumption of causal relationships somewhat speculative. The results do seem, however, to support the findings of other floodplain meadow research in many respects.

Hydrochory is known to represent a primary vector of propagules within floodplain systems, (Bendix and Hupp 2000), particularly amongst species with only a transient seed-bank, including fritillary, (McDonald, Bakker et al. 1996), and as the results here point to an increase in juveniles following wet years, (Figures 2.3 & 2.4), flooding would indeed seem to be important for recruitment.

Several studies have identified the importance of flooding for the creation of gaps or "safe-sites" for germination via the suppression of dominants, (Harper, Williams et al. 1965; Whited, Lorang et al. 2007; Kotowski, Beauchard et al. 2010), and also the particular significance of gaps for small-seeded species such as fritillary, which are often poorer competitors

in matrix habitats, (Grime 1979; Suding 2001; Hölzel and Otte 2004). Conversely, drought during the same period could also be seen to benefit juvenile numbers indirectly as parental seed would be more likely to be pollinated in drier weather, (Zhang 1983), and more seeds would ripen and remain viable.

The correlation between higher numbers of flowering adults and drought days in spring of the year prior to survey would seem to relate to the time when hormonal changes first trigger the development of the following year's flower bud. Zhang notes that the degree of flowering recorded in one season was linked in his study to the number of leaves and size of the bulb the plant had managed to produce the preceding year, and it would seem safe to assume that dry weather during the previous spring would indeed be favourable for the development of both foliage and bulb and thus also for the following year's flower.

The total fritillary population was found to be associated with between 10 and 35 annual flood days over the preceding three years. The decade in question was comparatively wet, which resulted in large germination peaks and an overall increase in population size. However the association

of flowering adults with drier weather in this study suggests that global warming might eventually have a negative impact on fritillary reproduction in the longer term, if it brings wetter springs in future.

It may be that further differences in the age-state spatial distributions of fritillary might also be detectable on this basis of lateral distance and connectivity to the water-channel, which could explain some of the patterns not explained directly by elevation or hydrology in this study, (Figure 2.17). Recent work undertaken by research staff within Floodplain meadow partnership found fritillaries to be absent from quadrats with rapid water-drop down rates in summer, and proposed that local differences in the soil profile in terms of moisture-retention capacity could explain some of the overall fritillary presence and absence patterns evident on the site, (Tatarenko 2013).

The ability of soils to retain water depends on its structure and texture, which is linked to flood-related sediment-deposition patterns, and which in turn represent a function of the distance and connectivity of the location in question to the active water channel, (Tockner, Malard et al. 2000). Studies have already highlighted a relationship between distance

and connectivity to channels and species distribution, (Cellot, Dole-Olivier et al. 1994; Tockner, Malard et al. 2000), and specifically, the role played by deposition of fine alluvia versus more rapidly draining, coarser, material, (Mouw, Stanford et al. 2009). It may be that such patterns involving substrate characteristics and/or localised compaction at the microhabitat scale could further explain certain contrasts in age-state distribution, for example, in relation to seedling versus adult survival rates during periods of drought and flood, though this requires further direct investigation.

The results of regressions regarding the most appropriate time-scale and length of variables with which to analyse ontogenetic patterns demonstrate that in the case of juvenile and flowering adult fritillaries, at least, recent, seasonal hydrology appears to represent the key hydro-period for analysis, (Figure 2.2), although both response-lags and the corresponding length of hydrological variables of most relevance can be seen to vary according to both age and key events during the life-cycle of *Fritillaria meleagris.*

Fritillary is a long-lived perennial, surpassing twelve years old in some cases, and it remains a possibility that numbers of vegetative adults could be better correlated with longer lags than the maximum five years included within this study. However, as the seedling and establishment phases are considered to represent the key bottlenecks for species recruitment on floodplains, (Kotowski, Beauchard et al. 2010), the juvenile and flowering adult associations would be likely to be of particular interest to conservation-management practitioners, and the results here did consistently highlight the importance of shorter, seasonal hydrological observations for these groups.

The occurrence of niche-shifts within the fritillary population and certain other life-history characteristics of the species could seem to represent co-existence strategies not incompatible with the theory of the "storage effect", outlined in Chapter 1, (Chesson and Warner 1981). They benefit differentially from fluctuations in conditions from year to year, with increases in numbers of juveniles in years following flood events, and increases in flowering adults following periods of dry conditions. They demonstrate differing spatial distributions, and are correlated with quite different hydrological variables. They also demonstrate the ability to buffer population growth, for example, via long life-span, dormancy and

stratification requirements etc.; all of which represent possible signatures of the "storage effect".

They could also be seen to demonstrate certain trade-offs in relation to tolerance of drought and flood versus competitive abilities; trade-offs which are widely considered to be of primary significance to species co-existence patterns on floodplains, (Tilman 1982; Keddy 1999; Silvertown, Dodd et al. 1999). The bulb of fritillary is renewed annually, and with each successive renewal it moves further down the soil profile, with juveniles positioned at approximately 1-3cm beneath the surface, sub-adults at 2-5cm, and adults at 5-8cm, (Zhang 1983). As adults possess deeper root systems than juveniles, they are likely to be more tolerant of drought and flood-related mechanical damage, and they also have the capacity to avoid unfavourable years via dormancy. Seeds and juveniles, on the other hand, are located closer to the soil surface, and are presumably able to grow more rapidly in gaps once temperatures rise to favourable levels in spring, thus avoiding some of the competition for light that is thought to limit slower growing species, or gap-dependent species in closed habitats, (Kotowski, Beauchard et al. 2010).

2.4.1 Caveats

The major challenge facing the project arose from the fundamental nature and complexity of the data. The data were not independent, and analyses undertaken singly could not satisfactorily partition the variation in the data attributable either to temporal or spatial autocorrelation. Accounts of alternative methods involving advanced multi-level modelling in "R" might possibly have proven informative in this respect, but locating and undertaking these techniques would have exceeded the time-scale of this project. Various attempts were made to try to remove the effects of autocorrelation within multiple regression, e.g. by the incorporation of year and quadrat as explanatory variables, but these methods were deemed unsound statistically and discarded. Previous studies have found, however, that autocorrelation issues, though important, are of comparatively minor significance in comparison to the primary environmental drivers of niche-shifts in grasslands, (pers. comm. J. Silvertown and G. Baquero, Open University), and the issue of repeat sampling was eventually resolved reasonably well by the inclusion of single-year analyses.

The selection of hydrological variables of most relevance to age-state dynamics was in part intuitive. The results of regressions using water-table depth values averaged across the site over the period in question, (*n = 10*), yielded much higher P and R^2 than regressions using the full hydrological dataset and *n = 1200* botanical samples, (e.g. Figure 2.2 versus Figure 2.9), which was thought to be due possibly to the presence of zeros or much lower total values in the full hydrological dataset. After a great deal of deliberation and repeat trial-and-error processes, the latter format was eventually selected, as the correlations identified using this method appeared to make more ecological sense, and appeared also to explain well certain patterns revealed in the following chapter, " Fritillary age-states and associates".

Future work that would be of benefit following the results of this study would include observational data from additional sites as well as other blocks on North Meadow; the incorporation of longer chrono-sequences; and soil profile data; the latter to investigate the possible significance of distance and connectivity to the water-channel in relation to patterns of age-state distribution.

Stage structured population models have also been found to represent an effective means of predicting both transient and long-term population behaviour within species; providing the basis for subsequent population management action, (Steiner 2012, Franco 2004), and could also prove informative in relation to the analysis of fritillary dynamics. Whereas in the past, integral models employing size as a continuous stage variable have commonly been undertaken when analysing plants, the results of this thesis indicate that the models most commonly applied to animal dynamics; i.e. discrete matrix models based upon age-state, would be appropriate when investigating niche-shifts within target plant-species.

2.5 Conclusion

Fritillaria meleagris was indeed found to display ontogenetic niche shifts within its population on North Meadow NNR; shifts which were particularly apparent between pre- and post-seed-dispersal stages and could be explained by gap requirements for recruitment from seed and the need for drier conditions for establishment.

Juveniles and flowering adults were seen to be correlated with shorter response-lags than other age-states, and with seasonal as opposed to annual hydrological variables, and the relative importance of timing and duration of these were found to vary according to both the age of the individual and also in relation to key events in the life-cycle of fritillary. Juveniles and flowering adults were found to co-occur significantly less often than could be expected by chance, and the total fritillary population was found to be associated with between 10 and 35 annual flood days over the preceding three years. The high degree of variation in hydrological values associated with quadrats of similar elevation, and the low R^2 of regression results, indicated that other factors not directly relating to elevation or hydrology could be contributing to some of the differences in age-state spatial distributions.

Continued monitoring of age-state fluctuations and further research of the role played by distance and connectivity to the water channel and associated soil profile characteristics, would greatly increase our understanding of any changes to population dynamics that may arise in future, and it is hoped, mitigate some of the adverse impacts associated with a rapidly changing climate.

Chapter 3

Fritillary age-states and associates

This chapter examines whether juveniles and flowering adults differ in terms of associated species and communities on North Meadow National Nature Reserve, Wiltshire.

Chapter 3: Fritillary age-states and associates

3.1 Introduction

If the environmental conditions experienced by each age-state are sufficiently different to result in observable niche-shifts in fritillary populations, then it is a reasonable hypothesis that other meadow species are also sensitive to these conditions; perhaps resulting in distinct associations between age-states and particular plant communities. The results of the previous chapter pointed to the occurrence of flooding prior to germination as the major correlation with the abundance of juveniles; supporting the theory that flooding enhances fritillary recruitment via the reduction in cover of competitors. It is hypothesised that these competitors are likely to consist largely of flood-sensitive, sward-forming grasses; with these species defined by their low indicator values for moisture, (Ellenberg 1979), and that a reduction in cover of these grasses following flood events will be found to correspond with an associated increase in juvenile abundance the subsequent year. It is anticipated that investigation of associate species and their ecological attributes will provide additional insight into patterns of niche-differentiation within

fritillary, and shed further light on recruitment mechanisms within this species.

3.1.1 Hypotheses to be tested:

(a) Differences in niche-requirements of juvenile versus flowering adult fritillaries can be detected on the basis of a corresponding difference in associated species and communities.

(b) Juvenile abundance in year *t* is correlated with reduced cover of flood-sensitive grasses during the growing season of year *t*-1, (i.e. prior to fritillary germination).

3.2 Methods

3.2.1 The datasets

Two primary botanical datasets were variously formatted within SPSS, CAP, (Community Analysis Package), (Henderson 2007), Minitab and Excel to investigate the hypotheses described above.

(a) With fritillary data derived from repeat surveys undertaken in April of each year, (outlined in Chapter 1), counts of juvenile and flowering adults were calculated for each of the 120 quadrats within Block 1 at Cricklade, for the period 1999 to 2008, following the method devised by Barkham, 1980). A second presence/absence file, (i.e. with quadrat values of 0 or 1), was also subsequently created.

(b) Botanical data derived from full quadrat species surveys undertaken annually in May/June was extracted from the Floodplain Meadows Database for the years (1998-)1999 to 2008, and three files were created; one representing % quadrat cover of all species recorded, a second using species presence and absence values, and a third detailing various facets of percentage grass cover, with each formatted to include 0 to 3 year time lags, (i.e. year: *t*, *t*-1, and *t*-2).

3.2.2 Age-states and associate species

To examine principal differences between the distribution of juveniles and flowering adults and associate species, a Decorana ordination plot was produced in CAP, using presence and absence data for species recorded in conjunction with fritillaries in fifteen or more samples.

To further define the contrast in community composition and boundaries, a Twinspan was undertaken, using presence and absence data for all species recorded with fritillary, (1999 to 2008). In order to highlight only the key distinctions within the dataset, a maximum of two divisions and two indicator levels were applied. The resulting four end-groups were then each displayed schematically in heat-maps, according to frequency of occurrence by quadrat over the period in question.

3.2.3 Twinspan end-groups and Ellenberg Values

Ellenberg Indicator values for moisture, (F), nutrients, (N), and pH, (R), for the end-groups were subsequently compared and Mann-Whitney U tests were undertaken to identify any significant differences between groups, (Ellenberg 1979).

3.2.4 Age-state communities and the revised NVC

The Twinspan end-groups for the fritillary file were compared with the noda derived from the recently revised National Vegetation Classification of floodplain meadow communities, (Wallace, pers. comm.), using a system of heat maps. Whereas the current study used only presence and absence data for species co-occurring with fritillary in Block 1, (1999 to

2008), the latter employed percentage cover for the entire dataset across the four Blocks at Cricklade, (1999 to 2012). It was anticipated, however, that despite these differences in datasets, comparisons would reveal similarities between the two accounts, supporting the hypothesis of a contrast in age-state community-membership.

3.2.5 Juveniles and cover of grasses

To examine whether juvenile abundance correlates with a decrease in cover of flood-sensitive grasses during the year prior to germination, which would support the theory of gap-dependent recruitment within fritillary following flood-events, stepwise multiple regressions were undertaken within SPSS, with quadrat juvenile counts as the dependent variable and various types of grass-cover figures, for year *t*, year *t*-1, year *t*-2, as the explanatory variables.

The latter included combined percentage cover of, (i) all grass species, (ii) grasses with an Ellenberg F value for moisture of 5 or less, and (i) the five indicator grasses, identified in Branch One of the Twinspan output. Only results from the latter analysis are described in full here. The selected variables were Arcsine-transformed prior to analysis. t-tests were then undertaken to examine any significant difference in the means of cover for

years *t*, *t*-1 and *t*-2 for samples containing juveniles versus flowering adults, and scatter graphs were produced to display the relationship between numbers of age-states and the cover of these grass species.

3.3 Results

3.3.1 Age-states and associate species

The degree of separation in position of juveniles and flowering adults on the Decorana plot reveals clear differences in terms of their relationships to associate species and to each other, (Figure 3.1). Axis one of the plot represents a complex gradient relating to nutrients and moisture, (see Figures 3.2 & 3.3), with *Agrostis capillaris* and *Luzula campestris*, and other "dry" or "poor" species tending to the left, with "wetter", or more nutrient-demanding *Carex* species etc on the right, and with juveniles and flowering adults situated intermediately left and right of centre respectively. The plot suggests, rather suprisingly, that juveniles occupy a slightly drier, more nutrient-poor position along the gradient than flowering adults, a pattern which is further supported by the results of Twinspan analysis.

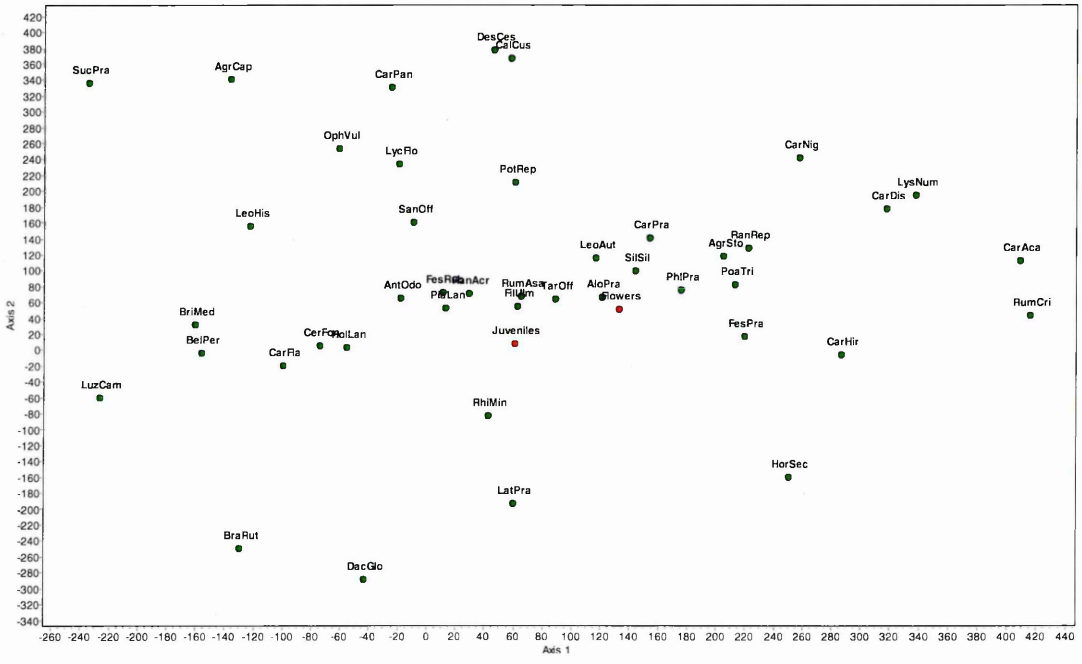


Figure 3.1 Decorana ordination plot displaying the distribution of juveniles and flowering adults and associate species.

(Eigenvalues of Axis 1 = 0.242, Axis 2 = 0.109)

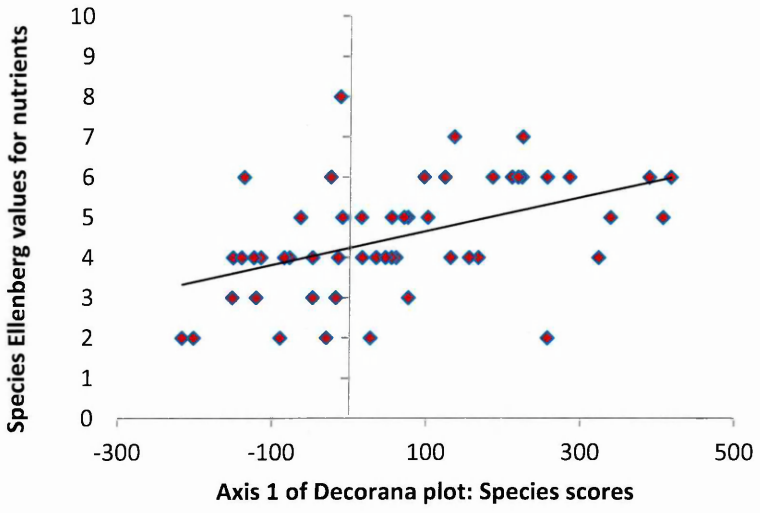


Figure 3.2 Scatter plot displaying the correlation between species scores for Axis 1 of the Decorana plot and their Ellenberg indicator values for nutrients, (R^2 = 0.2204).

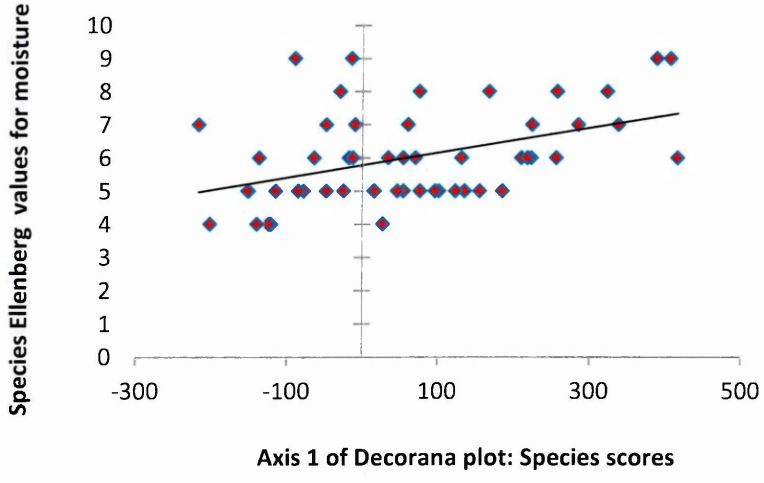


Figure 3.3 Scatter plot displaying the correlation between species scores for Axis 1 of the Decorana plot and their Ellenberg indicator values for moisture, (R^2 = 0.1844).

Figure 3.4 reveals the species composition of the four end-groups derived from Twinspan analysis, and Figure 3.5 displays the species indicative of each division. Juveniles and flowering adults became divided at the very first level of divisions, according to the frequency of their association with five particular grasses. These grasses were found to be mostly flood-sensitive species, with Ellenberg moisture values of 6 or below, (.e. *Festuca rubra*, *Bromus racemosus*, *Holcus lanatus*, *Anthoxanthum odoratum* and *Cynosurus cristatus*), and were negatively associated with the juvenile group, (2).

The heat maps displaying the quadrat distribution of the four groups in relation to the paleochannel, (Figure 3.6), indicate that the juvenile nodum, (Group 2), is generally posistioned further away from the channel than flowering adults, (Group 3), and optimum frequency of occurrence at the spatial scale also differs according to group. Group 2, associated with juveniles, has been the most frequent over the ten years, and has the largest spatial distribution within the Block.

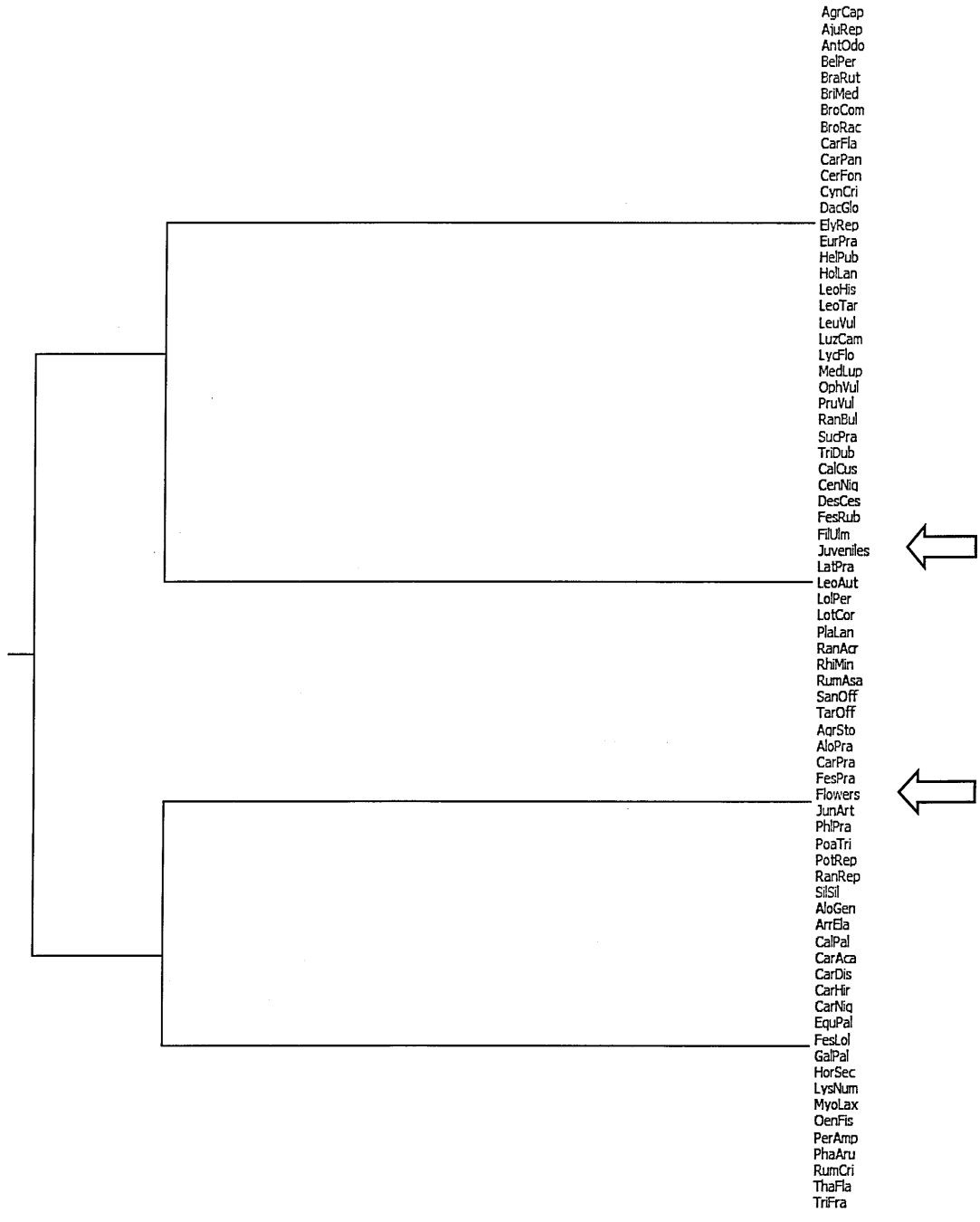


Figure 3.4 Twinspan end-groups 1- 4, derived from fritillary samples, (1999 to 2008, Block 1). Eigenvalues for Division 1 = 0.60, for Division 2 = 0.52, and for Division 3 = 0.42. Juveniles were found to be associated with Group 2, (blue arrow), and flowering adults with Group 3, (red arrow).

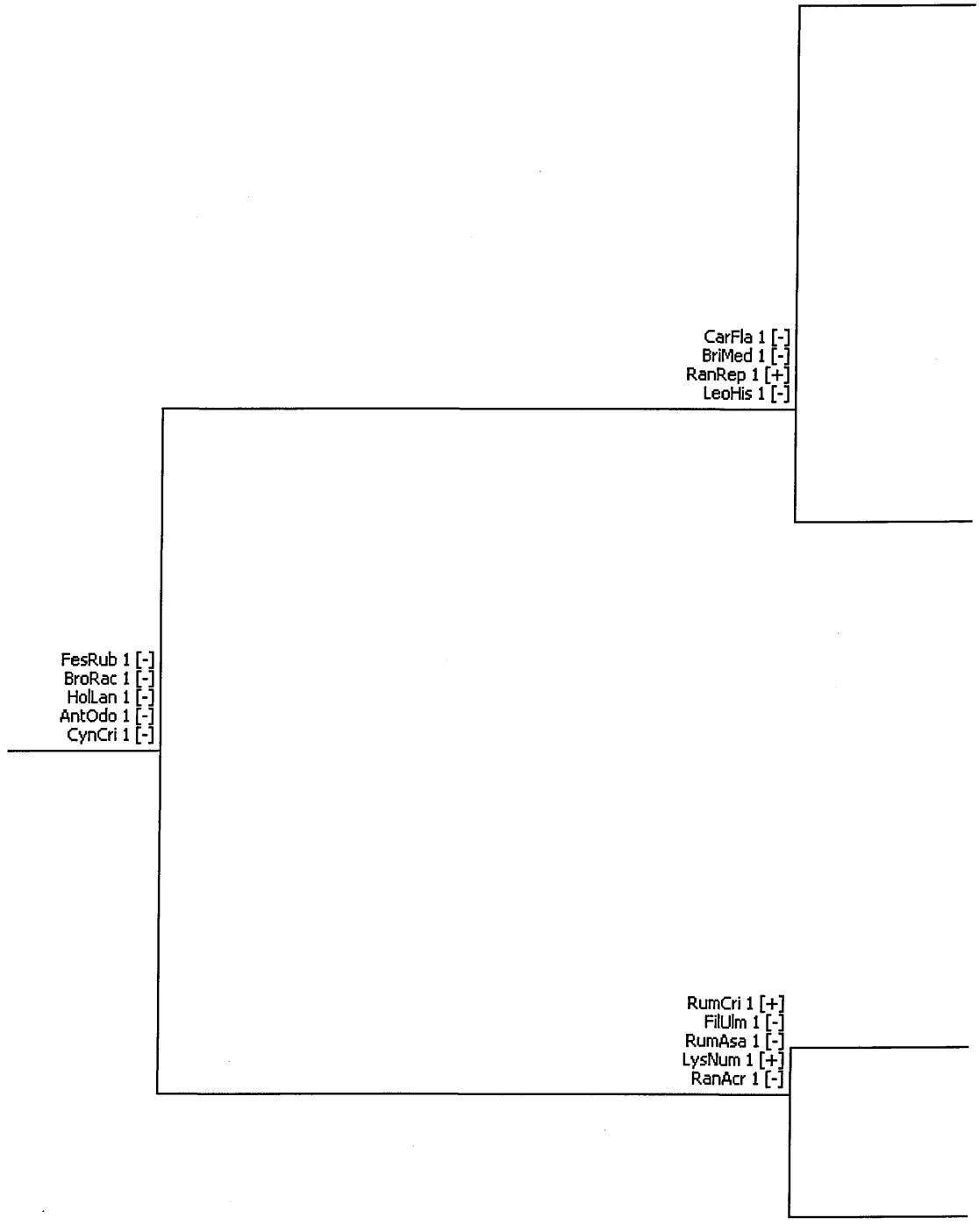
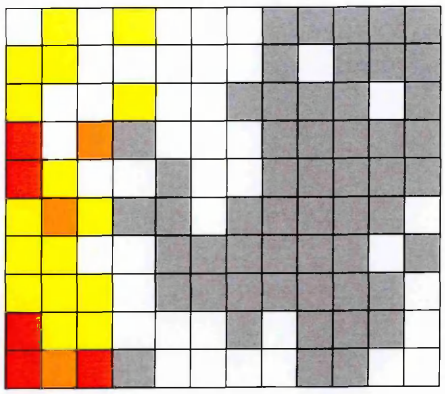
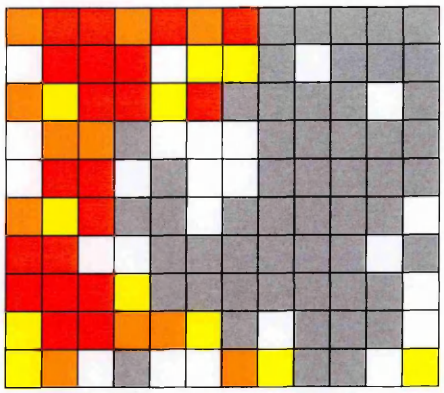


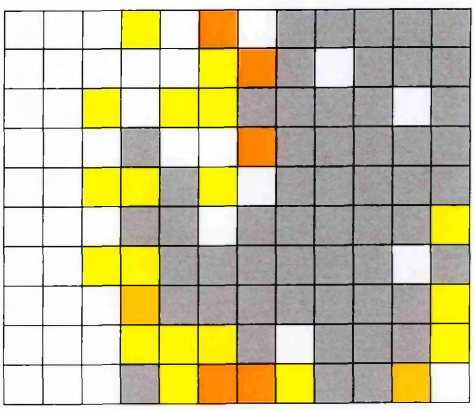
Figure 3.5 Twinspan division indicator species, derived from fritillary samples, (1999 to 2008, Block1).



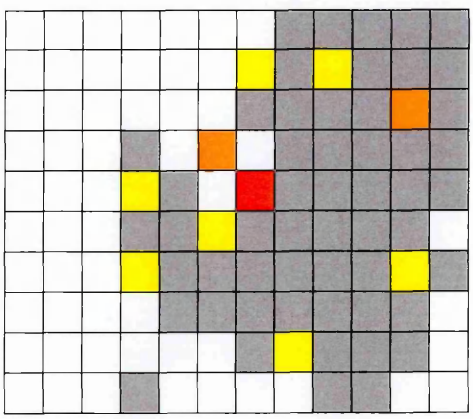
Group 1



Group 2 – (Including juveniles)



Group 3 (Including flowering adults)



Group 4

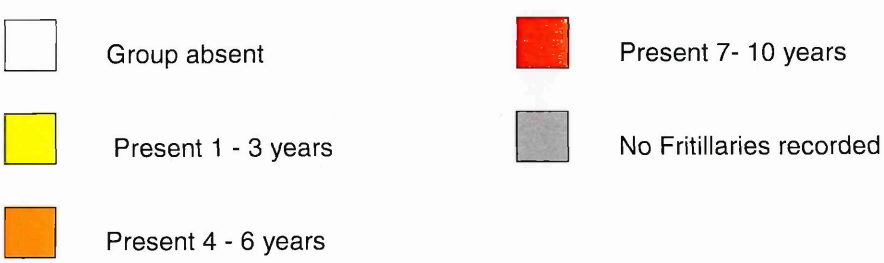


Figure 3.6 Schematic heat maps displaying the quadrat distribution of the four Twinspan end-groups and their frequency from 1999 to 2008.

3.3.2 Twinspan end-groups and Ellenberg Values

A Mann-Whitney U-test was performed to evaluate possible differences in Ellenberg values for moisture, (F), nutrients, (N), and reaction or pH, (R), between the four groups derived from the results of Twinspan analysis. Significant effects of group were found in relation to moisture and nutrients; indicating general gradients in these factors. The mean ranks of the juvenile and flowering adult groups for nutrients, were found to be 4.38 and 5.67 respectively, ($U = 29.5$, $Z = -2.3778$, $P=0.008$), and groups one and three, and one and four, also displayed significantly different values. Though juvenile and flowering adult group-differences for moisture were not significant at a $P<0.005$ level, groups one and four, two and four and three and four were found to differ significantly, (Figure3.8).

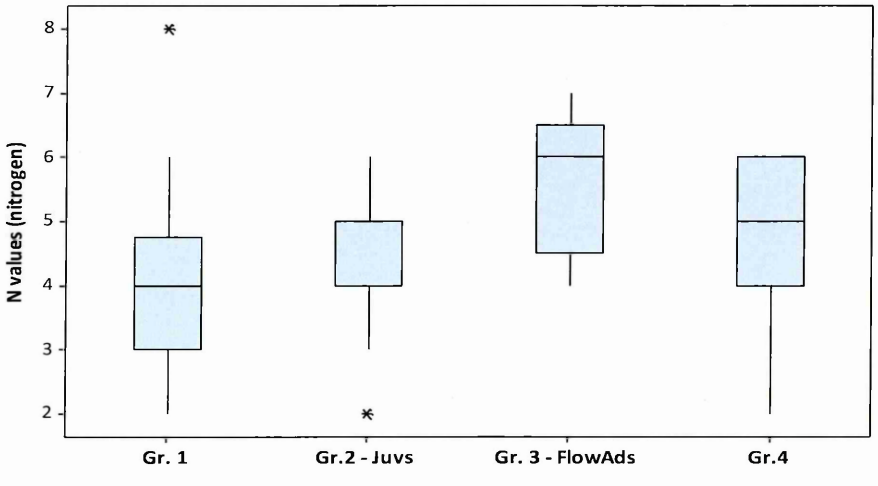


Figure 3.7 Boxplot displaying mean Ellenberg Indicator "N" values for nutrients for the four Twinpsan end-groups.

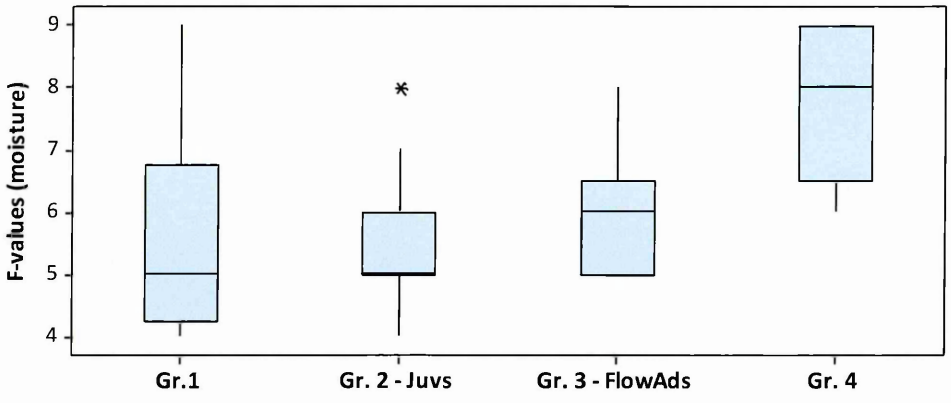


Figure 3.8 Boxplot displaying mean Ellenberg Indicator "F" values for moisture for the four Twinspan end-groups.

3.3.3 Age-state communities and the revised NVC

Comparisons between the distribution of the end-groups identified above, (Figure 3.9), and the noda compiled by the recently revised NVC classifications, (Figure 3.10), reveal a marked similarity between the juvenile and flowering adult groups, 2 and 3, and noda 6 and 5; coloured red and orange on both heat maps. This similarity suggests that the two age-states are associated with distinct sub-communities of NVC MG4; with juveniles related to the drier unit, nodum 6, and flowering adults correlated with the damper unit, nodum 5.

Figure 3.9 Fritillary end-groups

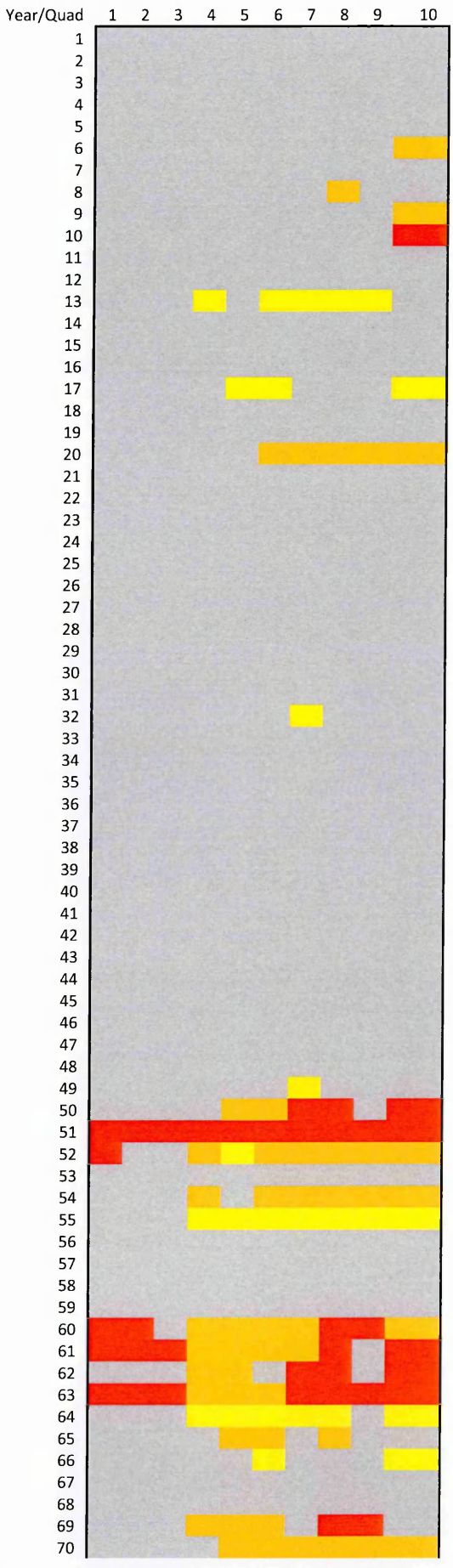
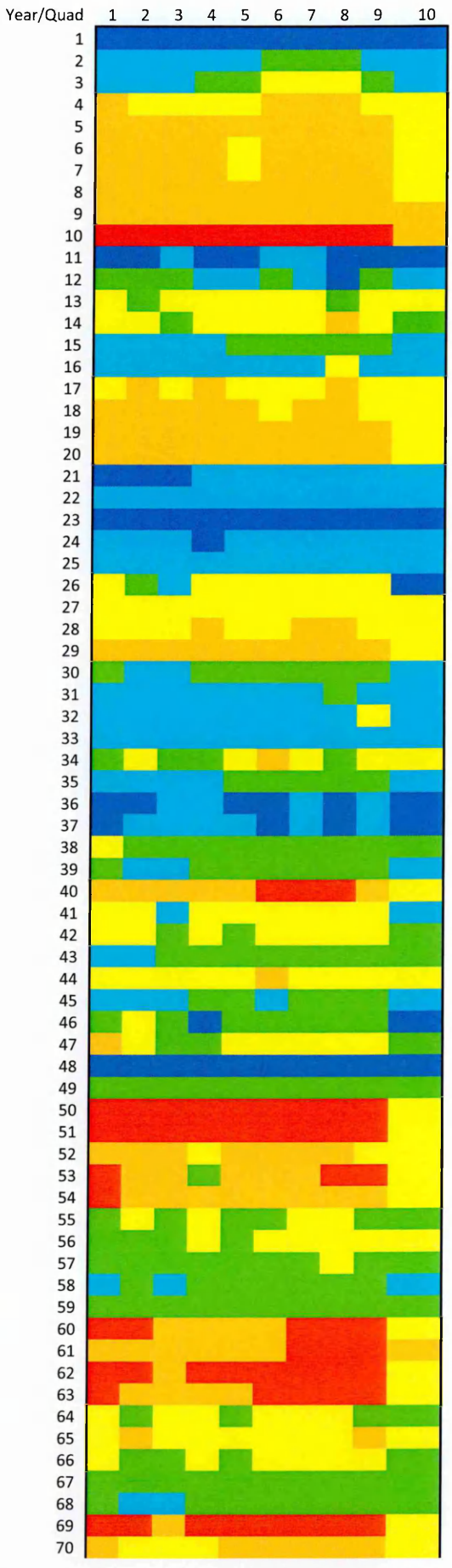
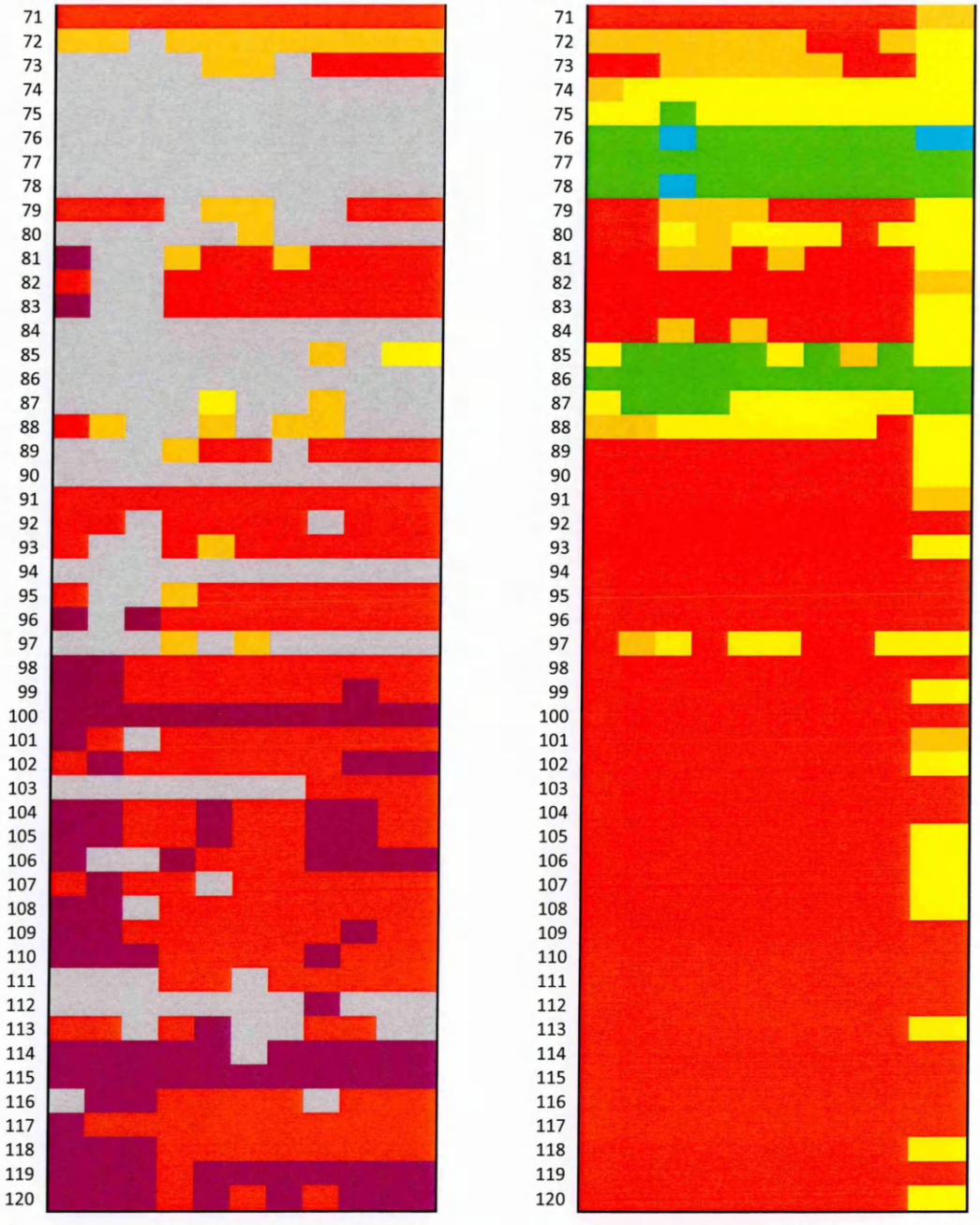


Figure 3. 10 Revised NVC noda





Group 1
Affinity to driest of Nodum 6

Group 2 (Juveniles)
Affinity to Nodum 6

Group 3 (Flowering adults)
Affinity to Nodum 5

Group 4
Affinity to Noda 3 & 4

No fritillaries recorded

Nodum 6: MG4 typical
(Dry, spp-rich; Dactylis glomerata)

Nodum 5: MG4
(Damper; Agrostis & Holcus)

Nodum 3: MG4
(Transition from Agrostis unit)

Nodum 4: MG4
(More referable to Agrostis unit)

Nodum 2: Agrostis-Carex
With some MG8 & S19

Nodum 1: Agrostis-Carex
With some MG13 and OV29

3.3.4 Juveniles and cover of indicator grasses

Results of regression revealed that juvenile abundance was found to be significantly negatively correlated with combined % cover of Twinspan indicator grasses in year *t*, (P<0.001), (Table, 3.1), whereas flowering adult abundance was found to be significantly positively correlated with cover of indicator grasses in both year *t* and *t*-1. t-tests revealed a significant increase in mean % cover of indicator grasses for juvenile quadrats between year *t* and *t*-1, (t = -1.870, P = 0.031), (Figure 3.11), whereas cover in flowering adult quadrats remained more or constant between years, (Figure 3.12). A similar pattern was found when comparing combined % cover of all grass species recorded, and also for those species with Ellenberg moisture values of 5 or less.

Included terms	B	t	R^2adj	P
Dependent = Juveniles (F = 9.84, df = 1,185, P<0.000)				
% Cover Twinspan grasses, Year: t	-0.476	-3.136	0.05	0.001

Table 3.1 Summary of enter regression model with quadrat juvenile counts as the dependent variable and % cover Twinspan grasses in year : t, using Arcsine transformed data, as the explanatory variable. The table gives the overall model fit and the parameter estimates for included terms.

Investigations revealed that numbers of juveniles peak at 1% cover of twinspan indicator grasses in year *t*, 13% in year *t*-1 and 18% in year *t*-2,

whereas flowering adult numbers peak at a much higher 15% cover in year *t*, (with 11% in year *t*-1 and 24% in year *t*-2).

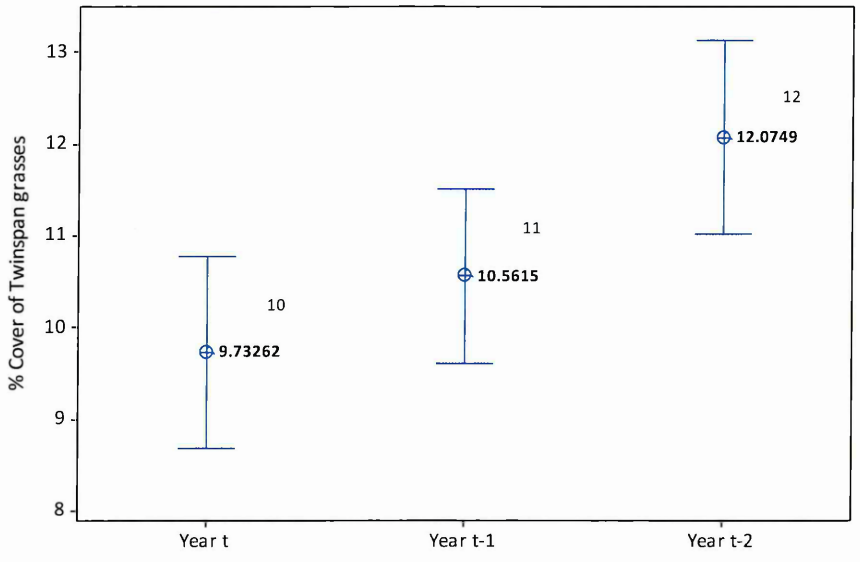


Figure 3.11 Interval plot of % cover of Twinspan grasses recorded in association with juvenile samples, (1998-) 2000 to 2008). Twinspan grasses are identified as the critical species responsible for the first branching of the Twinspan analysis, (displayed in Figure 3.5 and further explained in the text).

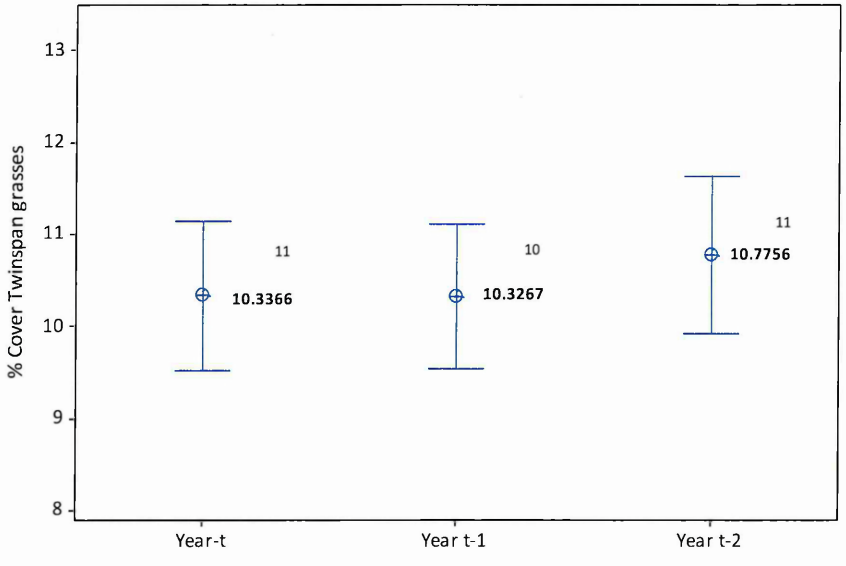


Figure 3.12 Interval plot of % cover of grasses within flowering adult samples, (1998-) 2000 to 2008. Twinspan grasses are identified as the critical species responsible for the first branching of the Twinspan analysis, (displayed in Figure 3.5 and further explained in the text).

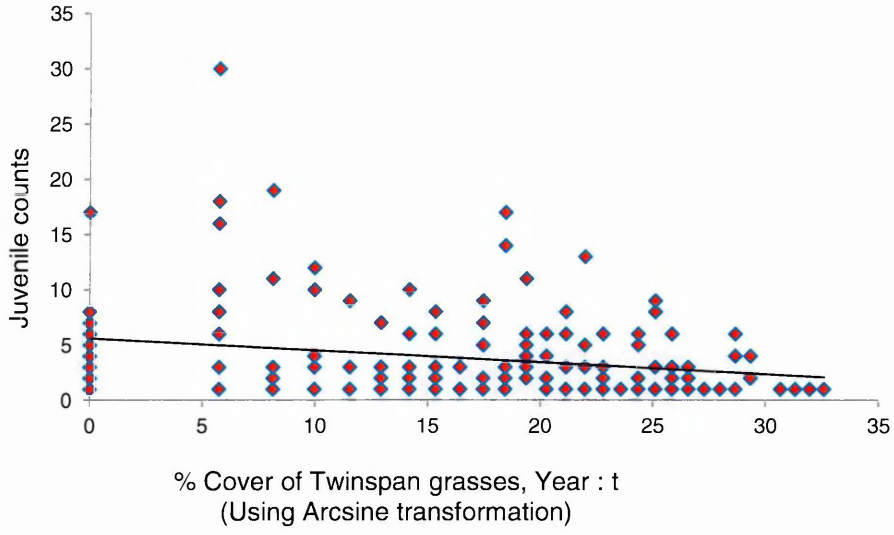


Figure 3.13 Scatter graph displaying the relationship between juvenile abundance and % cover of indicator grasses during year: *t*, using Arcsine transformed data. The linear trendline gave the following equation: $y = -0.1079x + 5.5994$, $R^2 = 0.0521$

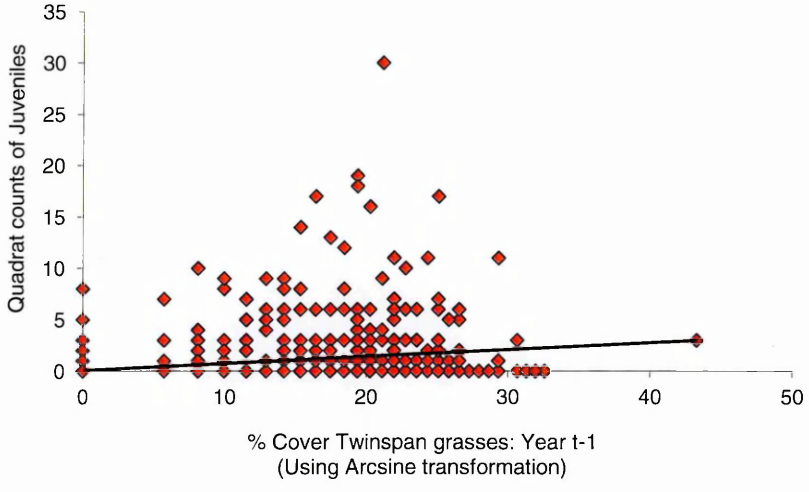


Figure 3.14 Scatter graph displaying the relationship between juvenile abundance and % cover of indicator grasses during year: *t*-1, using Arcsine transformed data. The linear trendline gave the following equation: $y = 0.0274x + 3.3693$, $R^2 = 0.0023$

3.4 Discussion

Whereas former documented accounts of juvenile versus flowering adult fritillary distribution have suggested a link between juvenile abundance and wetter habitats, (Zhang 1983), the results of this and the previous chapter indicate that not only were those findings not substantiated here, but that the reverse could be seen to be true; at least during the ten years in question on Block 1, North Meadow.

In the previous chapter, high interquartile range in water-table depth was found to be correlated with juvenile abundance only for the year prior to germination; i.e. with all active growth phases associated with generally dry conditions, (Table 2.2). Subsequent analysis of flowering adult distribution has revealed a relationship between numbers of this group and slightly wetter conditions than those experienced by juveniles, as expressed by; a) presence and absence patterns, (Figure 2.6), lower minimum quadrat elevation, (Figure 2.7), higher mean Ellenberg indicator values for nutrients and moisture of associated Twinspan group, and a negative association with (drier) Twinspan indicator species, in addition to a closer proximity of both flowering individuals and their associated end-group to the paleochannel; (Figures 3.1,3.2, 3.5, 3.9 & 3.10).

The drier Twinspan groups one and two, including core frequency of juveniles, consisted of a number of species that are known to colonise rapidly following flood events, such as *Leontodon autumnalis*, *Plantago lanceloata*, and the annuals *Bromus racemosus* and *Rhinanthus minor*; species which often display a marked drop in numbers in subsequent years if flooding does not recur. The bright yellow flowers of *Rhinanthus minor*, for example, often form distinct striping patterns along edges of the paelochannel the year after a flood-event, but no such patterning is visible the subsequent year if there is a return to more moderate conditions. The wetter Twinspan groups, three and four, on the other hand, contained a greater proportion of rhizomatous species and those capable of root-aerenchyma formation; traits known to be related to tolerance of flooding, (Evans 2004).

In the absence of planting experiments, it is very difficult to disentangle the effects of limitation imposed by seed-dispersal patterns, environmental constraints, and both positive and negative biotic interactions, in addition to any feedback processes that may be in operation in relation to vegetation and hydrology. The distribution of particular age-states could be attributable to a wide range of factors not directly relating to niche, including historical legacy and chance effects, or

other variables not directly analysed during this study, which could be further obscuring results. The cumulative evidence obtained suggests that flowering adults and their associated end-group are linked with slightly wetter, more nutrient-rich habitats closer to the paleochannel at this site during the period in question, but there could be several reasons for this. Factors such as soil profile characteristics could be playing a role; as has been found to be the case in relation to patterns of floodplain species distribution, elsewhere, (Mouw, Stanford et al. 2009). The ten years of the study period in question was also unusually wet, and the current distribution of flowering adults closer to the channel seems likely to be reflecting, at least in part, the patterns of spatial recruitment that occurred during the previous, much drier decade when river-levels were low; i.e. when juveniles were able to establish and survive to adulthood closer to the channel. This makes patterns of current age-state distribution rather difficult to interpret; in much the same way as ripples of sand on a sea-shore cannot be attributed to a single wave. Further research involving longer data-runs is required to clarify the role of historical legacy and the extent to which juveniles and flowering adults do in fact differ in their tolerance to flood.

The differences in nutrient values between the age-state groups was found to be the most significant of all U-test results, though again, the degree to which this reflects niche-differences or chance effects requires further investigation. Whereas, to my knowledge, there are no other accounts detailing such contrasts in age-state associates and communities within fritillary research, a handful of studies have established similar patterns in relation to other plant groups. One study of particular relevance, established a positive correlation between high nutrient-concentrations and reproductive biomass of mature old-field annuals, whereas seedlings were found to demonstrate no such limitation, (Parrish and Bazzaz 1985). The results of this project could also suggest that flowering adult fritillaries may have narrower nutritional niche-requirements than juveniles, as their associate end-group possessed the highest of all mean nutrient values, coinciding with a narrower spatial distribution. It is known that the best examples of NVC MG4 communities are associated with highly productive swards, (Gowing, Tallowin et al. 2002), and it seems likely that the other end-groups identified in Figures 3.4 & 3.5, occur in habitats that are either too dry or too wet to support the healthy microbial communities and enhanced N-release associated with peak numbers of the flowering adult group.

It had been anticipated that % cover of Twinspan indicator grasses within juvenile quadrats would display an anomalous drop in values during the year prior to the fritillary survey; in effect, that flood events of year t-1 would reduce the dominance of these species sufficiently to create gaps in the sward favourable for fritillary recruitment and enhanced germination the following year. Juvenile numbers were indeed found to peak in samples with lower cover of these grasses than flowering adults, i.e. 1% versus 15% cover, however, juvenile abundance was found to be best correlated with low cover of indicator grasses during the actual year of the fritillary survey, i.e. year: *t*, (Table 3.1), rather than year *t*-1 as anticipated, although a significant reduction in grass-cover was established between years *t* and *t*-1, (Figure 3.11).

These results might suggest that reduced competition during the establishment phase may be more significant to juvenile numbers than gap-formation prior to germination. Alternatively, it is also possible that some fritillaries could take more than one year to germinate, resulting in additional cohorts of juveniles present within a particular year. If this is the case, then the decline in cover of sensitive grasses between year *t*-1 and year t would indeed represent the trigger for the germination of these fritillaries, and account for the rather cloudy results of this analysis. It

could also be that the seasonal timing or cumulative impact of flooding on grass-cover over consecutive years might provide a better link with enhanced fritillary recruitment. The greatest drop in cover of these grasses, (and corresponding increase in numbers of juveniles), was seen in 2008 when there had been two wet years in a row, whereas both groups increased rapidly in 2002, following the floods of 2001. Further research involving longer data-runs, and incorporating variables quantifying between-year frequency of flood events and/or fritillary germination time-scales would be required to determine the exact temporal mechanisms behind these patterns of grass-cover dynamics and recruitment within fritillary.

3.5 Conclusion

This chapter investigated two primary hypotheses; i.e. that fritillary age-states display a difference in associated species and communities, and that juvenile abundance recorded in year *t* is negatively correlated with % cover of flood-sensitive grasses in year *t*-1. The first hypothesis was confirmed, and juveniles and flowering adults were found to be associated with distinct sub-communities of NVC MG4. Flowering adults were also seen to co-occur with species of comparatively higher nutrient and

moisture values than juvenile associates, and the flowering adult end-group also tended to be positioned closer to the paloechannel. A variety of factors including soil profile characteristics, historical legacy as well as possible differences in flood-tolerances between groups could be contributing to these differences in patterns of age-state distribution. Juvenile abundance was found to be better correlated with low cover of sensitive grasses during year: *t* rather than year *t*-1 as anticipated, although reduction in cover of these species between year: t and t-1 was found to be significant. Further research involving longer data-runs, the cumulative impacts of flooding on grass cover and more detailed accounts of the lengths of time required for fritillary germination could provide additional clarification of the temporal aspect of these relationships.

Chapter 4

Field experiment: The impacts of flooding on recruitment within key floodplain meadow species

This chapter investigates the impacts of flooding on recruitment by means of a fully factorial field experiment on Mottey Meadows, National Nature Reserve, Staffordshire, and North Meadow National Nature Reserve, Wiltshire.

Chapter 4: Field experiment: The impacts of flooding on recruitment within key floodplain meadow species

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4.1 Introduction

Results of database analyses during the previous chapters have suggested that recruitment within *Fritillaria meleagris* could be enhanced by flood events, which reduce the dominance of flood-sensitive grasses, and provide gaps for germination and establishment. However, little is known about the recruitment patterns of other key meadow species in response to flooding, particularly under field-conditions. Many meadow species display bimodal distributions in terms of hydrological preferences, (See Chapter 1), which could suggest that at one stage of their life-cycle they require wetter conditions than at another. The following chapter shall investigate whether the germination rates of *Fritillaria meleagris*, (Figure 4.1), *Leontodon autumnalis*, (Figure 4.2), and *Rhinanthus minor,* (Figure 4.3), species which all display such distributions, increase following flood-events, and by means of a factorial experiment, seek to test the following hypothesis;

4.1.1 Hypothesis

1. Germination of meadow species is enhanced by a treatment that simulates the effects of flood.

Figure 4.1 *Fritillaria meleagris* Figure 4.2 *Leontodon autumnalis* Figure4.3 *Rhinanthus minor*

4.2 Methods

A three-way factorial experiment was undertaken on North Meadow, Cricklade, and Mottey National Nature Reserves, between the spring of 2012 and the summer of 2013. This consisted of a planting experiment using mostly locally-sourced seed to quantify germination success, between species and between plots along a hydrological gradient, with two levels of competition. The major effects of flooding, i.e. vegetation die-back, were simulated by placing a metal plate over 50% of plots for a period of six weeks during the growing season. Half of the plots remained untreated and unsown, to provide a control.

4.2.1 Field-work

In spring 2012, nine x 50 m long transects on North Meadow and at Mottey were selected along hydrological gradients, using Google maps, and marked out using pairs of canes and the GPS, (Leica, RS1200, Switzerland). Twenty pairs of plots were set out every 2.5 m along each transect, with each plot about half a metre away from its corresponding pair.

One plot was covered with a custom-made, A4-sized, steel plate, (Figures 4.4 and 4.5), and secured using 4 x 7-inch, hooked, tent pegs hammered through holes in each corner of the plate. Its corresponding pair was kept without a plate. The choice of which pair would receive the treatment was randomised; by the throw of a coin. The plates were kept on the plots until early June 2012, just prior to the expected date of the hay cut.

Figures 4.4 & 4.5 Setting out the plates under flood conditions at Cricklade, spring 2012.

In May and June of 2012 seeds of *Leontodon autumnalis* and *Rhinanthus minor* were collected from both sites. *Fritillaria meleagris* seeds were collected only from North Meadow, as it is considered particularly rare at Mottey. (Permission to use Cricklade seed on Mottey was granted by the site's Natural England Manager, Mel Brown, on condition that every effort would be made to locate and remove the resulting seedlings following completion of the experiment). The collected seed was subsequently cleaned, counted and labelled, and hung up in open paper bags in a cool, dark potting shed out of the way of mice, on university premises.

The metal plates were removed from the treatment plots in early June to prevent any risk to the haymaking machinery, which is usually at work on the meadows from around the middle of June. When the plates were

removed, two tent pegs were immediately buried a couple of inches or so into the ground, directly beneath the top two corners of each plot, to ensure that each square could be re-located following the cut with the use of a metal detector and GPS.

The floods were so extreme that the cut was delayed by several weeks at Mottey, and at Cricklade it did not occur at all in 2012. At the latter site, it was eventually decided to exclude the wettest 4 transects from the experiment, and to strim the remaining five transects by hand prior to sowing. This was completed by early September.

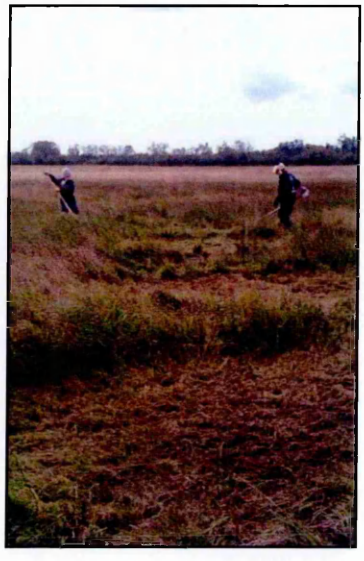

Figure 4.6 Strimming and raking the transects at Cricklade

In early August at Mottey, and by mid-September at Cricklade, forty seeds of *Leontodon,* forty of *Rhinanthus* and twenty seeds of *Fritillaria* were

sown per plot, using a pre-determined, randomised planting scheme. Seeds from each species were placed in a square of their own within the planting frame, to avoid cross-contamination; representing a total of three squares that were sown, and three that were seed-free, to provide a control within each plot. Figure 4.8 shows a single plot, and the planting squares inside the frame, and 4.7, the degree of flooding still evident at Cricklade, even in the comparatively drier transects.

4.7 Cricklade plots prior to strimming. 4.8 A4-sized planting frame, with 3 planting squares; one for each species.

The numbers of seedlings germinating on each plot were monitored in the autumn of 2012, with a final count taking place in April of 2013, and at Mottey, fritillary seedlings that had been sourced from Cricklade were removed.

Finally, a general seed viability test was undertaken. *Fritillaria* and *Rhinanthus* seeds had been kept in the freezer for 3 months over the winter of 2012, and in the spring of 2013, all three species were planted out in pots. (Ten pots per species were planted, with each pot containing 5 seeds per species). The pots were kept outside in the garden where they were exposed to normal climatic conditions, with some additional watering occasionally in hotter weather, and germinating seedlings were subsequently counted in the summer of 2013.

4.2.2 Datasets

Two primary datasets were variously analysed in SPSS, Minitab and Excel to determine the relationships between germination success, treatment and hydrology;

(a) A botanical file was created involving seedling counts of the three species planted in 2012 and presence/absence of treatment.

(b) A hydrological file involving water-table depth variables was produced. Daily figures were extracted from the Floodplain meadows database models outlined in Chapter 1, and calculated to produce Mean, Median and Standard Deviation in water-table

depth for: spring in year; t, and summer, growing season, winter and spring, for years; *t*-1, *t*-2 and *t*-3.

Analysis of variance and t-tests were used to analyse the relationship between seedling counts and treatment, and boxplots and confidence interval charts produced. Stepwise multiple regressions were undertaken, using the datasets listed above to investigate the relationship between seedling abundance and various aspects of the hydrological regime. Key variables were Log(n+1) transformed and scatter graphs subsequently produced to display the results.

4.3 Results

4.3.1 Germination rates under test- and field-conditions.

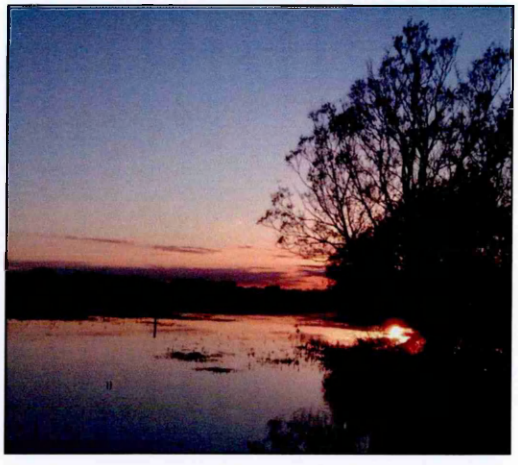

Figure 4.9 Cricklade floods 2012

The calendar year 2012 was the wettest in England since records began. The flooding lasted as long as nine months and well into the spring of 2013 on some parts of North Meadow, meaning little germination of any of the three species took place even on the comparatively drier experimental plots at this site, and the remaining five transects that had been sown there had to be dropped from the experiment.

At Mottey, germination of *Fritillaria meleagris* was also deemed insufficient for analysis and one transect had to be excluded as it became

apparent that GPS reception was too poor there for efficient re-location of the plots. Counts of seedlings from control plots were also later undertaken in transect 3.

Fortunately, the flooding had not been quite so extensive at Mottey as it had been at Cricklade, and although a few of the wettest plots, mostly in transect 3, remained bare late into the summer, overall, *Leontodon autumnalis* and *Rhinanthus minor* fared reasonably well here. The photographs below display plots from two transects of contrasting hydrology at Mottey; one subject to prolonged flooding, Figure 4.10, and the other comparatively drier, Figure 4.11, with both photographs taken in late summer. Both plots had received a plate treatment and sown seed, but show very different results, demonstrating that little germination takes place when flooding surpasses a critical threshold, (Figure 4.10). In total, from both sites, data was collated from 44% of the original experimental plots.

Figure 4.10 A plot from transcect 3.

Figure 4.11 A drier transect

Results of the germination test indicated that approximately 30% of the seeds collected and grown on in pots had germinated, whereas about 15% had germinated under field-conditions. Slightly more *Leontodon* germinated in pots than *Rhinanthus*, (38% v. 28%), and slightly more *Rhinanthus* germinated under field-conditions, (15% v. 12%), though neither set of differences were found to be significant, (P=0.25).

Significant differences were found between numbers of seedlings from control versus sown squares in transect 3, (t= -7.77, P<0.001), with a mean of 0.3 seeds recorded from the control, and 7 from sown ones, (Figure 4.14). Slightly more *Leontodon* germinated in control plots than *Rhinanthus*, though not significantly so, (P=0.082). *Rhinanthus* counts

were significantly higher than *Leontodon* in sown squares, (t = -4.13, P< 0.001, DF = 61), (Figure 4.15).

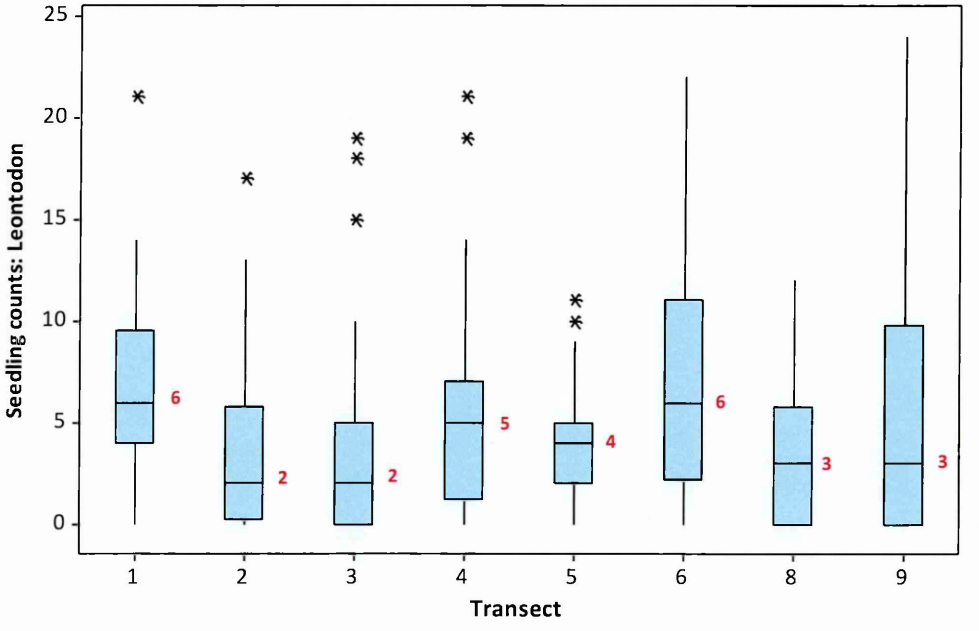

Figure 4.12 Boxplot displaying the median, (highlighted in red), outliers, and interquartile range in numbers of germinated seeds of *Leontodon autumnalis* recorded in field conditions from Mottey according to transect, (includes any derived from seed-rain and persistent seed).

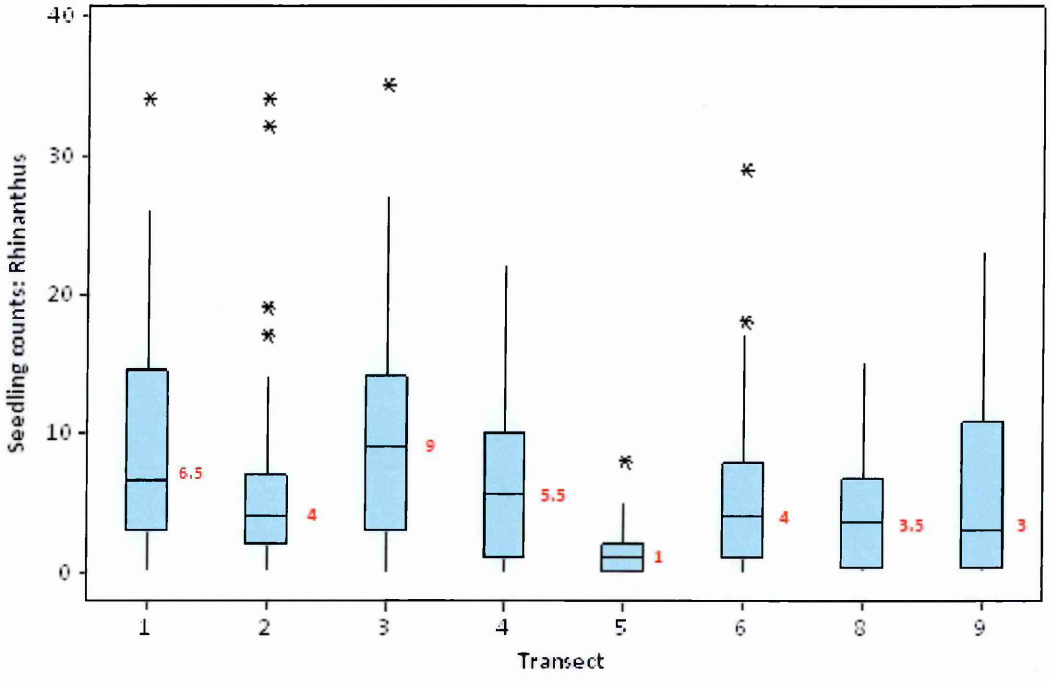

Figure 4.13 Boxplot displaying the median, (highlighted in red), outliers, and interquartile range in numbers of germinated seeds of *Rhinanthus minor* recorded in field conditions from Mottey according to transect.

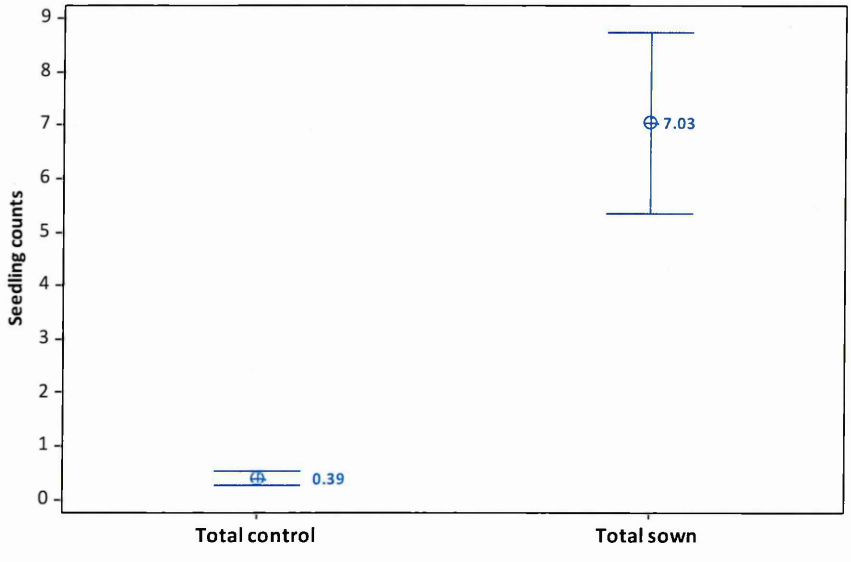

Figure 4.14 Interval plot displaying the 95% Confidence Interval for the mean numbers of seedlings recorded from control versus sown squares, in transect 3. (Mean highlighted in blue). Significant differences between germination recorded on sown versus control squares; (t = -7.77, P< 0.001, DF = 79).

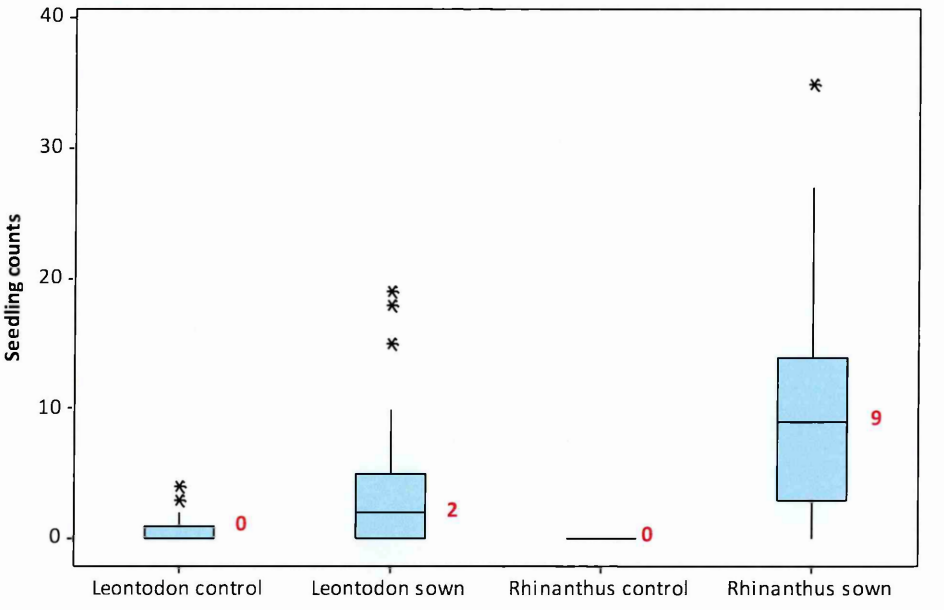

Figure 4.15 Boxplot displaying the median, (highlighted in red), outliers, and interquartile range in numbers of *Leontodon* and *Rhinanthus* seedlings counted from control versus sown squares, in transect 3. Significantly less *Leontodon* germinating on sown squares than *Rhinanthus;* (t = -4.13, P <0.001, DF = 61).

4.3.2 The results of plate-treatment.

Two-way Anovas and t-tests were performed to investigate; a) the degree to which variance in *Leontodon* and *Rhinanthus* counts could be explained by plate-treatment and transect, and b) whether their mean counts were significantly different. Plate treatment and transect were both found to be significant for both species at level P<0.001, (Table 4.1 & 4.2). Differences in F-values indicated that the presence of a plate explained comparatively more of the observed variance in *Leontodon* counts, and that transect

explained more of the observed variation in *Rhinanthus* counts, (F=19.8 versus 12.42, and F = 7.46 and 3.83), with regressions for the full models giving an adjusted R^2 value of 10.65% for *Leontodon* and 15.08% for *Rhinanthus*, respectively.

T-tests confirmed that mean *Rhinanthus* seedling counts were significantly higher than *Leontodon* on squares with no plate, (t = 3.30, P=0.001, DF = 274), and that significantly more *Leontodon* germinated on squares receiving the plate treatment, (t = 4.25, P<0.001, DF = 310), (Figure 4.16).

Source	DF	F	P
Plate	1	19.18	<0.001
Transect	7	3.83	<0.001
Total	319		

Table 4.1 Analysis of Variance for *Leontodon autumnalis*

Source	DF	F	P
Plate	1	12.42	<0.001
Transect	7	7.46	<0.001
Total	319		

Table 4.2 Analysis of Variance for *Rhinanthus minor*

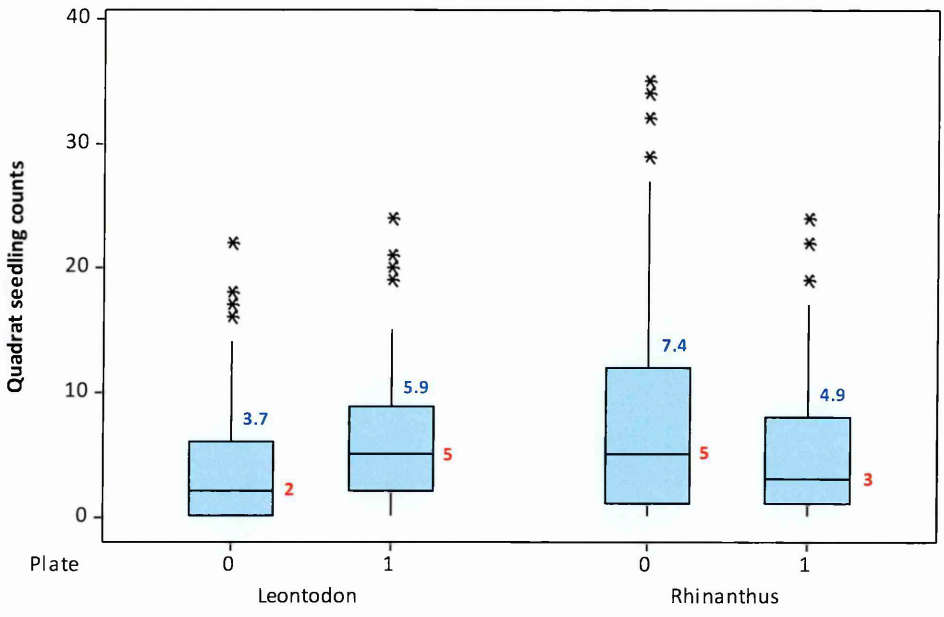

Figure 4.16 Boxplot displaying the median, (highlighted in red), interquartile range, outliers, and mean, (highlighted in blue), numbers of seedlings counted from quadrats without/with the plate treatment, (0/1). Significantly more *Rhinanthus* than *Leontodon* germinated on squares with no plate, (t = 3.30, P = 0.001, DF = 274), and significantly more *Leontodon* than *Rhinanthus* germinated on squares with a plate, (t = -4.25, P< 0.001, DF = 310).

4.3.3 Correlations between species and hydrology

The results of stepwise multiple regressions using hydrological explanatory variables, indicated that for both species, the presence or absence of plate was the most important variable associated with their abundance, followed by transect in the case of *Rhinanthus*. When investigating the relative importance of the hydrological variables alone, results suggested that peak numbers of *Leontodon* were positively

correlated with standard deviation in water-table depth; in spring of the year prior to survey. Interestingly, *Rhinanthus* abundance was found to be negatively correlated with Standard Deviation, (P<0.001), when the latter variable was entered singly in a regression. The most significant hydrological variable overall for this species, in terms of adjusted R^2, was found to be median water-table depth; in Spring of the year prior to survey, with which it was positively correlated, (Table 4.3, and scatter graphs 4.17 and 4.18).

Included terms	B	t	R^2adj	P
i. Dependent = Leontodon (F = 14.291, df = 1,318, P<0.001)				
StDev. water-table depth, Spring, yr: t-1	0.0005	3.78	0.04	<0.001
ii. Dependent = Rhinanthus (F= 10.930, df = 1,318, p<0.001)				
Median water-table depth, Spring, yr:t-1	5.17E-05	3.306	0.03	0.001

Table 4.3 Summary of enter regression models with plot counts of *Leontodon* and *Rhinanthus* seedlings as the dependent variables and Log(n+1)-transformed Standard Deviation and Median water-table depth, during Spring of the year prior to survey as the explanatory variables. The table gives the overall model fit and the parameter estimates for included terms.

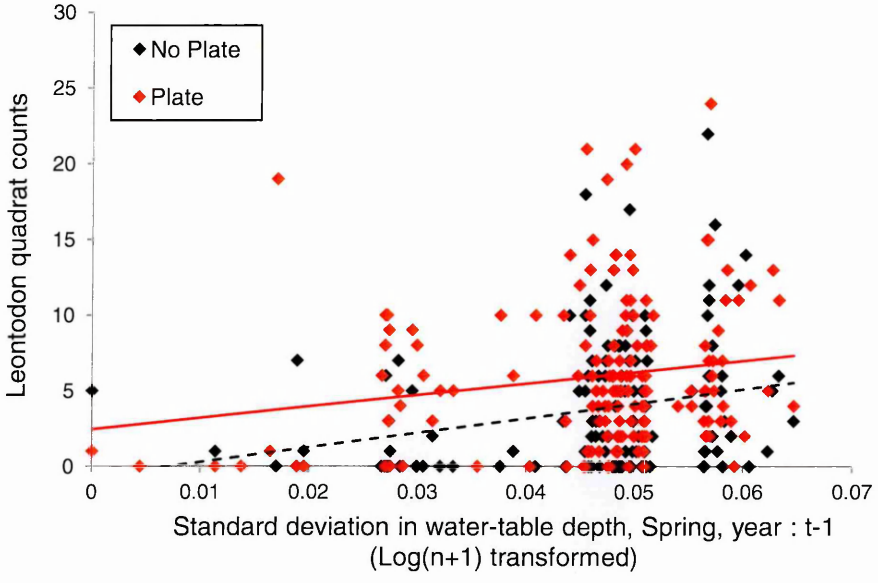

Figure 4.17 Scatter graph and linear trend lines displaying the relationship between abundance of *Leontodon autumnalis,* with and without a plate and standard deviation in water-table depth, using Log(n+1) transformation, during Spring, year: t-1.

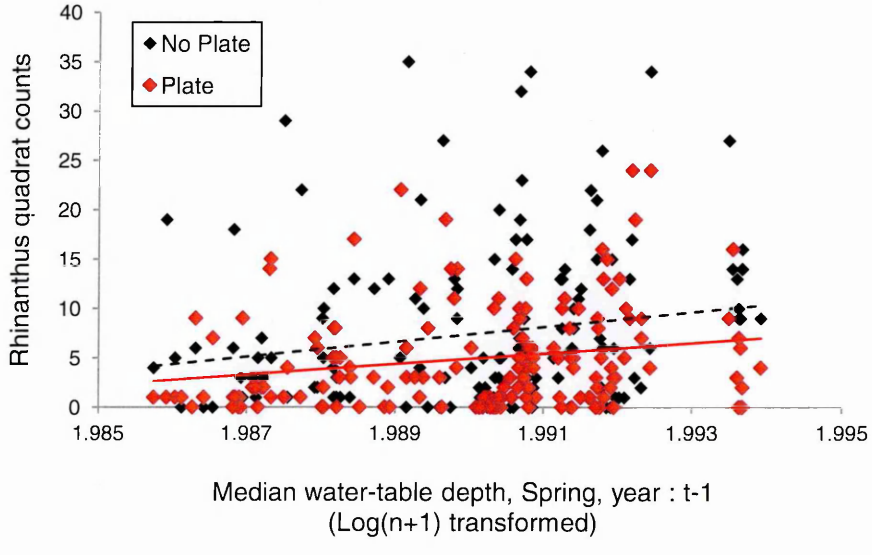

Figure 4.18 Scatter graph and linear trend lines displaying the relationship between abundance of *Rhinanthus minor*, with and without a plate, and median water-table depth, using Log(n+1) transformation, during Spring, year: t-1.

When total seedling counts recorded at each value of median water-table depth were plotted together, no evidence could be found to support the theory that *Leontodon* prefers wetter conditions than *Rhinanthus*, as described by Ellenberg, (Figure 4.19); at least with regards to germination stage-requirements.

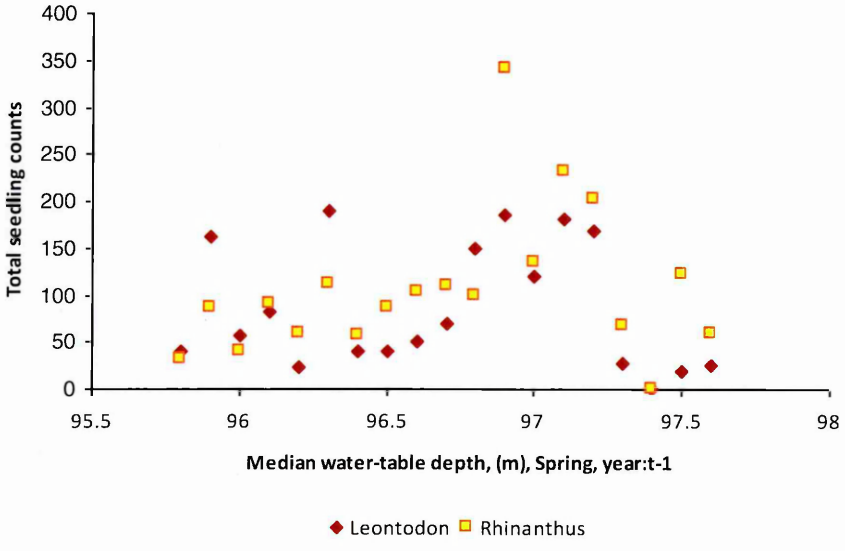

Figure 4.19 Scatter graph displaying abundance of *Rhinanthus minor* and *Leontodon autumnalis* and median water-table depth.

4.4 Discussion

Despite the difficulties posed by the weather, the results of the field-experiment indicate that germination is indeed affected by plate-

treatment simulating flood-effects, but the direction of response is different between the species, and depends on the types of survival strategies exhibited by the species in question.

Leontodon autumnalis is a species most characteristically associated with "short-turf and open ground", and it is known to be fairly intolerant of shading, (Grime, Hodgson et al. 1989). Previous research has suggested that germination within this species is at least partially inhibited by tall leaf canopies, (Gorski 1977), with most seedlings recorded either from gaps arising in the autumn following summer die-back, or in early spring of the following year, when co-existing plant cover is low. This gap-detection strategy within *Leontodon* was also observed during this field-experiment, and results of analyses confirmed the significant increase in seedling counts on plots where competition had been removed, (Figure 4.16).

Rhinanthus minor, on the other hand, displayed a negative correlation with the presence of a plate, (Figure 4.16). *Rhinanthus* is considered to be an obligate hemi-parasite under field conditions, and it seems likely that the low abundance of seedlings on plots that had received a plate was due to the absence of its required host-species following treatment.

Certain differences were found in terms of germination rates between *Leontodon* and *Rhinanthus* when; (a) potted up in the garden, (b) in control pots in the field, (c) in sown plots in the field, although only the latter were established as being of significance, (Figure 4.15). Overall, results showed that *Leontodon* numbers were slightly higher than *Rhinanthus* in the home-germination test, (38% versus 28%), similar in unsown plots, (0.5 versus 0.2), but significantly lower when sown in the field, (with a mean of 3.8 versus 10.2). Further research is required to establish definitive germination rate-ranges for these species before conclusions could be made, although it is clear that *Rhinanthus* counts were higher than *Leontodon* in sown field conditions, though both species were sown in identical numbers and subject to the same climatic conditions.

Speculatively speaking, the pappus of *Leontodon* would make the seed-head considerably more mobile than that of *Rhinanthus*, and from field-observation, it seems likely that a much greater proportion of *Leontodon* could be lost from plots due to wind, rain and flooding under field conditions, than were lost from the comparatively more sheltered habitat of a garden pot; which could explain the significantly higher proportions of *Rhinanthus* germinating from planted seed in the field.

However, *Leontodon* can flower as late as October, (in contrast to August for *Rhinanthus*), and its seed can remain viable, on, or just below the surface of the ground for a year or so, whereas *Rhinanthus* seed does not. Additional *Leontodon* seed could also have easily been transported by wind from other sites on the meadow onto the control plots; which together could have offset some of the losses under field conditions, and accounted for the similar mean control counts to *Rhinanthus*, (0.5 versus 0.2).

Ellenberg gives *Leontodon* a value of 6 on the hydrological scale and *Rhinanthus* a drier value of 5, although this study found no evidence to support this contrast. Rather, results tended to concur with the opposite conclusions of Grime's extensive study, (Grime et al, 2008), which found, that, in England, at least, *Leontodon* is most associated with moist, but not waterlogged soils, whereas the range of *Rhinanthus* often extends to wet soils, and is absent from habitats subject to prolonged drought , (Grime, Hodgson et al. 1989).

The results of regression established a positive correlation between *Leontodon* abundance and standard deviation in water-table depth in

spring of the year prior to survey, but a negative correlation between the same hydrological variable and *Rhinanthus*, (Table 4.3).

High standard deviation would seem to point to conditions that are, at some stage during spring, sufficiently wet to reduce competition prior to germination, but at another stage, dry enough to ensure parental flowering, and it appears that *Leontodon* and *Rhinanthus* display different responses to some aspect of this variable. *Rhinanthus* was found to be most strongly correlated with high median water-table depth during the same period, suggesting that on average it prefers wetter conditions throughout the spring prior to germination, and indeed, in the wettest transects at Mottey, e.g. transect 3, (Figure 4.12 and 4.13), *Rhinanthus* displayed a median plot count of 9 versus the 2 seedlings of *Leontodon*.

This poses the question of why *Rhinanthus* should display greater germination rates in plots that had not received a plate, (i.e. simulating areas that had not been flooded), but conversely, also do well in the wettest areas. Results of analysis examining the relationship between both these species and median water-table depth, (including Figure 4.18), showed a lot of scatter and noise, and other graphical outputs, (not displayed here), also proved inconclusive. It may be that the closer

correlation of *Rhinanthus* with transect established during regressions could indicate additional, unmeasured factors contributing to its abundance in certain areas. It could also be that some aspect of flooding-related disturbance benefits *Rhinanthus*, but only when not so severe as to result in the complete removal of its primary hosts. What is clear, is that this study found insufficient evidence to confirm that *Leontodon* seedlings are found in wetter habitats that *Rhinanthus*, certainly during the germination stage. Further detailed research of germination rates between species under test and field-conditions, and survival-rates between age-states along the same hydrological gradient, would help to clarify these questions, and hopefully prove useful for the long-term of success of related sowing and restoration projects.

4.5 Conclusion

The original hypothesis that germination is enhanced by plate treatment simulating flood effects was confirmed for *Leontodon autumnalis*, but was found not to be the case with the hemi-parasite, *Rhinanthus minor*, which displayed a large increase in seedling counts on plots without a plate. This was considered to be due to its requirement for host species, notably grasses.

Leontodon abundance was found to be correlated with standard deviation in water-table depth during spring of the year before survey, and *Rhinanthus* with median water-table depth. No evidence was found to indicate that *Leontodon* is associated with wetter habitats than *Rhinanthus*, as described by Ellenberg, at least in terms of germination-stage. Further research of germination and survival rates along the hydrological gradient is recommended for both juveniles and subsequent age-states to identify the full range of requirements of target species.

Figure 4.20 Mottey Meadow NNR, Summer 2013

Chapter 5

General discussion

This chapter summarises the work from previous chapters and recommends future research questions

5 General Discussion

5.1 Introduction

The study had three primary aims; a) to determine whether ontogenetic niche shifts are occurring along a hydrological gradient within *Fritillaria meleagris* and selected meadow species, b) to quantify the key hydrological regime, in terms of timing and lags in response, of most relevance to the study of age-state niche-requirements within fritillary and selected species, and c) to investigate the possible relationship between a reduction in cover of flood-sensitive grasses and enhanced recruitment within fritillary.

5.1.1 The occurrence of ontogenetic niche shifts within *Fritillaria meleagris*.

Although abundance of fritillary adults was found to be associated with predominantly dry conditions, and the correlation of sub-adults with drought experienced two years prior to survey suggest that seedlings also prefer this general type of regime, significant differences were established

in relation to both the timing and duration of hydrological variables of most relevance to individual age-state dynamics, and also in relation to the role of flood. In contrast to other groups, interquartile range in water-table depth during spring of the year prior to germination was established as the key factor associated with juvenile abundance when analysed directly; implying micro-site limitation and enhanced recruitment in flood-related gaps.

Subsequent investigation of possible differences in age-state associate species and communities also revealed that further niche-segregation might be occurring in response to factors not directly quantified during this study. Juveniles and flowering adults were found to co-occur in less than half of the recorded samples and demonstrated a significant degree of spatial separation. Flowering adults were recorded generally closer to the water-channel, and their associate species possessed higher nutrient and slightly higher moisture values. The age-states also clearly differed in relation to community membership; with juveniles associated with a comparatively drier sub-community of NVC MG4, generally situated further away from the channel. As flowering adults were mostly recorded in smaller numbers and within a smaller spatial subset of locations than

juveniles, it was suggested that this species exhibits a niche contraction through ontogeny.

Although no significant difference was found between juvenile and flowering adult plot-elevation, the hydrology of plots at identical elevations was found to vary widely, due, it was considered, to factors such as distance and connectivity to the active water channel. Such factors are known to affect soil texture and structure, determining both the degree of aeration and moisture-retention capacities of the soil, and thereby influencing species distribution, (Mouw, Stanford et al. 2009). It seems likely that such factors involving soil profile and/or other historical legacy effects could be contributing to the different spatial distributions of age-states, but how these interact with other variables, namely hydrology, remains unclear. Further investigation is required to establish whether these spatial patterns reflect differences in tolerance-levels, and represent additional drivers of niche-segregation within fritillary.

Over the period in question, (1999 – 2008), peak numbers of all fritillary age-states occurred in plots receiving an annual average of between 17 and 20 flood days per year, over the preceding three years. This

represents a moderately dry regime maintained over some period of time, but in addition to an upper threshold of flooding, interestingly, these figures also point to a lower one for all age-states.

5.1.2 Recommendations for further research

- Further research of ONSs within fritillary would benefit from the inclusion of variables encompassing distance and connectivity to the water-channel, soil profile characteristics and legacy effects, which could be playing an additional role in differential age-state distribution within this species.

- Research investigating the upper and lower limits of fritillary age-state tolerances to factors including soil compaction, flood and drought would enable niche-requirements to be further defined.

5.2.1 The relevance of gaps for recruitment within *Leontodon autumnalis* and *Rhinanthus minor*

Germination of *Leontodon autumnalis* was significantly higher on plots that had received a treatment simulating flood; suggesting micro-site limitation during the recruitment stage. As the established niche of the

adult population demonstrates abundance also within drier localities, (Gowing 2002), (outlined by the graphs of bimodal distribution in Chapter 1), these results parallel those of fritillary and imply that ontogenetic niche shifts are also occurring within this species. *Rhinanthus minor,* on the other hand, displayed higher rates of germination on plots that did not receive a treatment, pointing rather to the lack of sufficient host-species following extensive flooding as a key limitation. Similar findings describing *Rhinanthus* density as a function of host density have documented elsewhere, (Hulst, Shipley et al. 1987). Interestingly, no support could be found to suggest that *Leontodon* prefers wetter conditions than *Rhinanthus*, as previously claimed. In fact there was some suggestion that the reverse could be true, certainly in relation to germination requirements, though this was not a focus of the study and results of initial tests were inconclusive. The results generally support the view, however, that in cases where ONSs are known to exist, single values for whole-species environmental preferences are unlikely to be indicative of the full range of conditions required for long-term survival.

5.2.2 Recommendations for further research

- Future research of relevance for the effective conservation of target species could involve a study of germination, reproduction and survival rates along key gradients within target habitats, to enable the full range of whole-species requirements to be fully met and understood.

5.3.1 The relevance of timing: key hydrological periods and lags in age-state response.

Spring of the year before survey was identified as being of particular importance to germination within all three species investigated, and was also found to represent the critical time for numbers of flowering adults within fritillary, with results suggesting that the following year's flower bud-development may be triggered at this stage. When analysing the correlates with fritillary sub-adult, vegetative adult and whole-species abundance dynamics, results pointed to a longer time-span of variables required. Temporal lags in species response clearly vary according to both floristic measure and the importance or sensitivity of particular life-history

events, which should be taken into account when analysing species-environment relationships.

The multiple regression methods employed by this study to select hydrological variables of key relevance to age-state dynamics could not on their own partition the effects of temporal and spatial autocorrelation, and although additional methods were used that solved this issue reasonably satisfactorily, additional statistical techniques including multi-level or stage structured models could serve to further strengthen and clarify the species-environment relationships investigated here.

5.3.2 Recommendations for further research

- Studies and initiatives aiming to define the niche of target species would benefit from full testing of ontogenetic responses to driver variables of various lengths and timing.

- Further research involving multi-level modelling and a broader range of statistical methods could provide additional information

and a greater degree of certainty when investigating species-environment relationships.

5.4.1 Gap-creation and cover of flood-sensitive grasses.

Abundance of juvenile fritillaries was indeed found to be correlated with a reduction in cover of flood-sensitive grasses, but in year: t, rather than year: t-1 or t-2, as anticipated; although cover in year: t was found to be significantly lower than in t-1. It was concluded that the cumulative impact of successive floods on flood-sensitive grasses might best account for the gap-creation dynamics on these meadows, though the proportions of fritillary seeds germinating in years: 1, 2 and 3 following dispersal have not been definitively established as yet under field-conditions and further work is required to investigate these temporal dynamics.

5.4.2 Recommendations for further research

- Further studies involving longer data-runs and variables quantifying the cumulative impacts of flooding on grass cover, plus research establishing fritillary germination rates over successive years, under both test and field conditions, would seem likely to provide additional insight into the temporal dynamics of gap-creation and its relationship to recruitment.

5.5 Discussion

The growing frequency of extreme climatic events and difficulties in maintaining traditional farming techniques within our current socio-economic climate, have made the need to understand the mechanisms of community assembly, co-existence and diversity within floodplain meadows a major focus of research, as concepts such as these form the scientific basis for conservation strategies and adaptive management, enabling resources to be targeted effectively, (Pickett, Cadenasso et al. 2001). Ontogenetic niche shifts are thought to represent one of the most significant of such mechanisms, but studies involving plants are few, and

their occurrence within UK floodplain meadows had not been substantiated prior to this study.

The results of this project suggest that ontogenetic niche shifts are indeed a frequent occurrence within UK floodplain meadow communities, but are species-specific, and detected in two of the species investigated during the span of this research. Fritillary age-state abundances were seen to be correlated with quite different hydrological variables. Juveniles and flowering adults were found to occupy significantly different spatial locations, and were, for the first time, seen to be associated with distinct ranges of associate species and NVC sub-community types. Both *Fritillaria meleagris* and *Leontodon autumnalis* demonstrated microsite-limitation with enhanced germination in gaps where cover of flood-sensitive grasses had been reduced or eliminated following floods; indicating an increase in competitive fitness during later stages of ontogeny.

Most previous research of ONSs involving plants, (Quero, Gomez-Aparicio et al 2008, Eriksson 2002), has found no evidence for niche-shifts at the dispersal to germination stage as revealed here, with the exception of Miriti's study of bur-sage *Ambrosia dumosa* in the Colorado desert,

(2006). In her research, successful germination was found to be positively related to occurrence under a canopy of adults, with adult performance diminished when in proximity to each other; indicating a switch from facilitative to competitive interactions post-germination.

Facilitative interactions during the seed to seedling stage were also documented in this project's experiment, where abundance of seedlings of the hemi-parasite *Rhinanthus* were clearly related to host-density. Interestingly, survivorship of *Rhinanthus* to adulthood has been found to be negatively correlated with surrounding biomass in other studies, (Van Hulst et al, 1987), suggesting that ONSs in response to competition for light may also occur within this species, but between later age-states than investigated during the time-scale of this project.

Although the stricter gap-requirements during the germination stage of fritillaries would tend to suggest a niche expansion within this species during ontogeny, (supporting the conclusions of Parrish and Bazzaz, 1985, Quero et al, 2008), the narrower spatial distribution of flowering adult fritillaries would also seem to point to a contraction in niche-width during later stages, (such as found by Eriksson, (2002)); though the latter could

simply represent a function of fewer numbers and/or interacting ontogenetic niche-constraints, and the issue remains inconclusive.

The roles of niche and dispersal processes within community assembly were seen to vary in importance along flood-disturbance gradients, with fluctuation in the timings and magnitudes of such events seen to account for driving growth and restructuring processes within these habitats, (Toogood, 2009). Though flooding is clearly a key filter for meadow-community assembly, several researchers have pointed out that the use of hydrological variables alone have rarely been sufficient to predict short-term trajectories, (Trowbridge 2007), and projects aiming to reinstate the "correct" hydrology and nutrient balance following habitat destruction in restoration schemes has often been ineffective, (Matthews and Endress 2010). The results of this study suggest that many of these difficulties may have arisen, at least in part, by employing hydrological variables of inappropriate types or duration.

This project highlighted that both the direction and rates of response to hydrology and disturbance can vary significantly between age-states and species according to differential life-history strategies, physiologies and

morphological adaptations, (Gerisch, Dziock et al. 2010; Scheffer 2010). Spring of the year prior to survey was seen to represent the hydrological period of key relevance to germination success within all three species investigated, (supporting the findings of Zhang, 1983), but also to flowering success within *Fritillaria meleagris*, and the remaining fritillary age-states displayed longer lags; each in response to different variables. These results confirm the need for comprehensive testing of environmental variables prior to analysis.

Results supported the view that changes in hydrological regime and subsequent competitive interactions may be mediated through plant functional traits, (Grime 1979; Keddy 1992; McGill, Enquist et al. 2006; Gaucherand and Lavorel 2007; de Bello, Lavorel et al. 2008; Villeger, Mason et al. 2008; Toogood and Joyce 2009), with dispersal traits being of particular importance following extreme flood events. It was observed that the robust seeds of *Rhinanthus minor*, well-adapted to hydrochory, gave rise to a marked abundance along the upper edges of water-channels following floods, presumably in areas where sufficient host-species are able to persist, and the long flowering season and wind-dispersed seeds of *Leontodon autumnalis* is known to be of particular benefit to recruitment occurring under temporally and spatially variable conditions.

The paucity of germination from the field-experiment and from the annual Fritillary count on North Meadow NNR in 2013 was thought to be a consequence of extreme flooding beyond the bounds of what is considered to be "normal" variation, pointing to a possible threshold in recruitment and a breakdown in the "storage effect" within this species. Although annual counts subsequently returned almost to pre-flood levels in 2014; highlighting its very effective dormancy strategy, it seems very likely that the lack of flowering adults and high levels of juvenile mortality experienced during the 2013 flood-year will have resulted in proportionately low numbers of juveniles and sub-adults in 2014.

To predict how successful this species will be in adapting to long-term climate change in future, it would be informative to establish the number of years each age-state can remain dormant and the population remain viable as a whole, when faced with a reduced juvenile population and the absence of substantial reproduction from seed. Data collated from recent seasons could equip future researchers with a ready-made, large-scale "natural experiment" and a unique opportunity with which to further investigate the themes of resilience and threshold dynamics within floodplain meadow species.

5.5.1 Implications for conservation management

Although the project employed data from one site only and results are therefore not directly transferable between sites, certain general inferences may be made with regards to ONSs and fritillary-environment relationships that will hopefully be of interest for conservation management and restoration purposes.

Traditionally managed floodplain meadows containing the NVC MG4 community are characterised by flooding that is regular in winter, very occasional in spring and absent during the summer months, followed by a hay-cut and grazing of aftermath, (Gowing,2002). The findings of this project suggest that from the point of view of the fritillary population, conservation initiatives would benefit from aiming to restore the disturbance regime, rather than establishing recommended absolute values of water-table depth, (the latter usually derived from annual averages), as the requirements for successful germination and flowering within this species are distinct, with each responding to naturally fluctuating seasonal and/or interannual events that may not occur every year.

Retoration projects involving the spread of green-hay as a source of propagules have found that, with the exception of *Rhinanthus minor*, NVC MG4 component herbs often fail to establish and grasses can tend to dominate, (http://www.floodplainmeadows.org.uk). This project found juvenile fritillary germination to be negatively correlated with cover of grasses in year t, (with optimum numbers associated with 1% cover of grasses versus the 12% for flowering adults), and therefore plots with low values for these grasses, (and the appropriate flooding regime for successive generations), would seem most likely to support new cohorts of germinating fritillary. Wet or dry springs, respectively, would be likely to result in increased germination and flowering adults the following year, and three comparatively dry years in a row would have a good chance of resulting in high total fritillary numbers.

In samples on North Meadow, juveniles were most often associated with core NVC MG4 species, several of which were annuals and ruderals, and comparatively "dry"; including *Plantago lanceolata*, *Ranunculus acris*, *Rumex acetosa*, *Sanguisorba officinalis*, and *Centaurea nigra*, whereas flowering adults were commonly recorded with a slightly "wetter" nodum; and included species such as *Agrostis stolonifera*, *Cardamine pratensis*, *Alopecurus pratensis*, *Juncus articulatus* and *Ranunculus repens*. Future

monitoring of additional sites could reveal whether this is a widespread general pattern, indicating a difference in tolerance levels, or, conversely, if other localised factors can explain this distinction.

Recent comprehensive testing of the use of Ellenberg Indicator values has confirmed that, within certain parameters, this system can provide a valuable tool for habitat assessment, (Schaffers et al 2000). However, the findings of this study suggests that such values may not accurately reflect the full range of intergenerational requirements of individual species. The differences in relationships between hydrology and juvenile versus flowering adult fritillaries revealed by this study indicate that the latter require comparatively dry conditions, although Ellenberg assigns a high value of 8 for moisture to the species as a whole, and similar discrepancies were established in relation to *Rhinanthus* and *Leontodon* requirements and described accounts. Ellenberg values are derived from all recorded occurrences of species, where all age-states are given equal weight. This could undoubtedly cloud distinct age-state habitat-preferences, bias the needs of the most abundant age-states over other less represented ones, and makes no account of possible requirements for isolated environmental events, or interannual fluctuation in conditions; risking inappropriate interpretation of species ecology.

As the occurrence of ontogenetic niche shifts are central to our understanding of plant population and community dynamics, (Miriti, 2006), it is recommended that the full range of intergenerational requirements of target species of high conservation value be identified and documented through experimental research; thereby improving our knowledge of species ecology and helping to ensure that conservation management actions have the best possible chance of success.

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